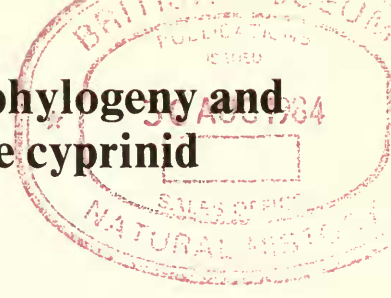


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# A review of the anatomy, taxonomy, phylogeny and biogeography of the African neoboline cyprinid fishes

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## Introduction

In a review of the bariliine cyprinids (Howes, 1980), the genus *Engraulicypris* which previously had contained ten species was recognized as monotypic, its only species, *E. sardella* confined to Lake Malawi. Those species formerly included in *Engraulicypris* were re-assigned to the genera *Neobola* Vinciguerra, *Chelaethiops* Boulenger, and *Rastrineobola* Fowler, with the accompanying statement that they formed a monophyletic assemblage whose close relationships were with Asian phoxinines rather than with African bariliines (Howes, 1980:196). Later, Howes (1983) modified these views and included *Neobola*, *Chelaethiops* and *Rastrineobola* among the bariliines, naming them as the neoboline lineage (see fig. 2 in Howes, 1983). Although a suite of supposed apomorphies characterizing the three genera were given (Howes, 1980:195), together with lists of their contained species no detailed generic diagnoses were presented. The purposes of this paper are:

1. To give diagnoses of the genera *Neobola*, *Chelaethiops* and *Rastrineobola* and establish a new genus to contain two species formerly assigned to *Neobola*. The characters used in these diagnoses are, for the greater part, those involving cranial anatomy. From previous studies (Howes, 1978; 1979; 1980; 1981; 1982; 1983) and from out-group comparisons made in the course of this work it is clear that in cyprinids cranial characters provide the most pertinent information at all levels of investigation.

2. To review the taxonomy of the included species. Although the neoboline cyprinids are abundant in many lakes and rivers of east, central and west Africa, they are, as compared with other cyprinids poorly represented in collections both in terms of sample sizes and geographic range. The species are small-sized, pelagic zooplanktivores and form an important part of the diet of many piscivores (see Fryer & Iles, 1972; Lowe-McConnell, 1975; van Oijen, 1982). Previous taxonomic reviews have been those of Poll (1945) and Whitehead (1962) but these authors relied for the most part on data compiled from the literature. Almost

all the material on which this review is based is from the collections in the British Museum (Natural History), and types of nearly all species have been examined. Other specimens used are from the collections of the Central African Museum in Tervuren (MRAC) and the American Museum of Natural History (AMNH).

3. To confirm the supposed monophyly of the neoboline genera and to consider their intra- and interrelationships.

4. To consider, in the light of their phylogenetic relationships, the biogeography of the neoboline taxa and some broader issues of African biogeography.

## Diagnoses, anatomy and taxonomy of the neoboline genera

### *NEOBOLA* Vinciguerra, 1895

*Neobola* is characterized by the articulation of the lower jaw extending posterior to the centre of the orbit; a dorsally channelled, broad supraethmoid; 10–12 olfactory lamellae on each half of the nasal rosette; 4–7 short gill-rakers on 1st ceratobranchial; small pectoral axial scale with a fleshy ventral border; pharyngeal teeth in two rows, 5·3; scales small with 5–8 parallel radii, 37–41 in the lateral line; the lateral line gently decurved anteriorly and running close to the ventral margin of the trunk with a wave-like irregularity along the caudal peduncle; swimbladder divided by a deep constriction into short anterior and posterior chambers, the posterior extending to above the pelvic fin.

CONTAINED SPECIES. *N. bottegi*, *N. fluviatilis* and *N. stellae*.

### Cranial anatomy

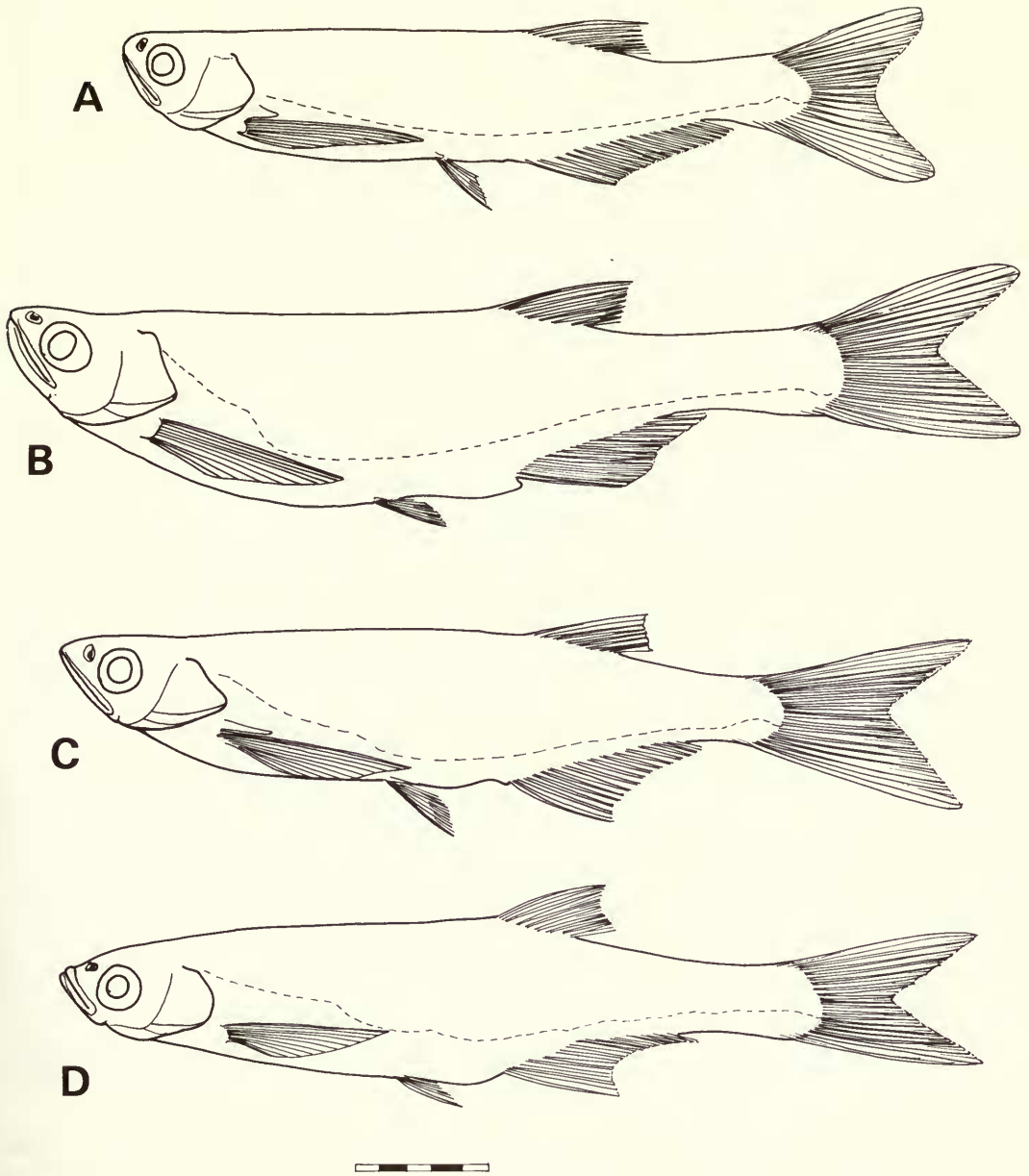
*Osteology* (Figs 2–4). The *ethmo-vomerine bloc* is short, deep and triangular, its anterior border has a sloped indentation. The supraethmoid is narrow-waisted, the lateral margins of the bone are concave and raised, thereby forming a shallow dorsal channel; the frontals overlay the posterior border of the bone. The vomer has a concave anterior border which projects only slightly beyond the overlying mesethmoid. Each lateral ethmoid is truncated with the dorsal part of the lateral wall extending anteriorly (Fig. 4).

The *frontal sensory canal* runs along the margin of that bone and is raised above the level of the supraorbital. There are 4 or 5 sensory canal pores; the first is extensive, and all open somewhat laterally. The *nasal* is long and curved into the concavity of the supraethmoid border; it has no dorsal pores.

The *infraorbitals* are deep (Fig. 6), the sensory canal of the 1st runs along the ventral border of the bone, but in the 2nd, 3rd and 4th the canal runs along the orbital border. In the 5th, the canal passes through the centre of the bone. The *supraorbital* is broad and long, narrowly separated from the 5th infraorbital.

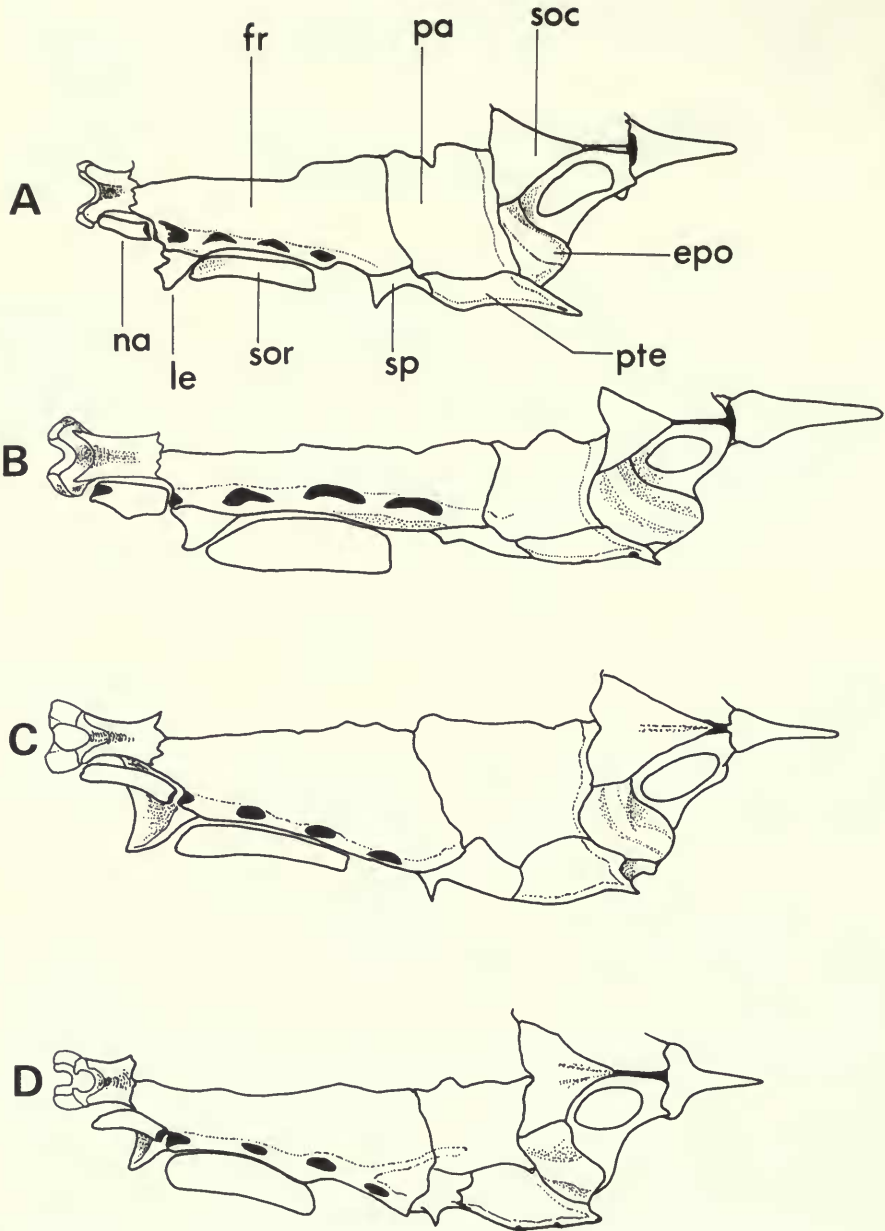
The *orbitosphenoids* are connected with the parasphenoid *via* a narrow septum; the *pterosphenoid* contacts the ascending process of the parasphenoid across a narrow area of bone. There is a small lateral *sphenotic* process which provides the greater part of the dilatator fossa. The *prootic* is large with the anterior trigemino-facialis foramen narrowly separated from its anterior border; there is a long lateral commissure. The posterior myodome is completely floored by the parasphenoid and basioccipital. A small posttemporal fossa is formed by the posterior separation of the *dermo* and *autopterotics*. The *supraoccipital* is small, lacks a crest, and is confined to the posterior slope of the cranium.

The *jaws* are long, the posterior tip of the maxilla extends to, or beyond the centre of the orbit. The maxilla is slender with a low mid-lateral (palatine) ascending process which curved laterally (Fig. 7). The posterior part of the maxilla is spine-like with only a slightly expanded tip which extends to below the centre of the orbit. The premaxilla is slender with a low ascending process and slightly concave ventral border. The dentary is shallow with a long, high, backwardly sloped coronoid process; the dorsal margin of the dentary is gently convex (Fig. 8). The anguloarticular is short with a slightly concave dorsal border.



**Fig. 1** Representatives of neoboline genera: A, *Neobola bottegi*; B, *Mesobola brevianalis*; C, *Chelaethiops bibie*; D, *Rastrineobola argentea* (drawn from a Lake Kioga specimen). All genera have 7 branched dorsal fin rays (rarely 6 or 8) I 10 pectoral rays; I 7 pelvic rays and 10+9 principal caudal rays.

*Suspensorium* (Fig. 9). The hyomandibula is broad and its dorsal facets are deeply separated. There is a weak lateral flange, its recess providing the insertion of the *levator arcus palatini* muscle. The ento- and metapterygoids have a marked concavity toward the midline; the dorsal border of the entopterygoid is straight, that of the metapterygoid is markedly concave. The palatine is laterally compressed, its anterior head forming a tripartite process, the medial spur of which overlies the concavity between the mid-lateral and anterior ascending maxillary processes.



**Fig. 2** Crania, in dorsal view: A, *Neobola bottegi*; B, *Chelaethiops elongatus*; C, *Mesobola brevianalis*; D, *Rastrineobola argentea*. epo=epioccipital; fr=frontal; le=lateral ethmoid; na=nasal; pa=parietal; pte=dermopterotic; soc=supraoccipital; sor=supraorbital.

*Branchial arches.* The ceratobranchials bear 4–8 short gill-rakers. Pharyngeal teeth on the 5th ceratobranchial are caniniform, arranged in two rows (5.3).

The *operculum* (Fig. 9) has a shallow concave posterior border, the ventro-posterior part of the bone being attenuated.

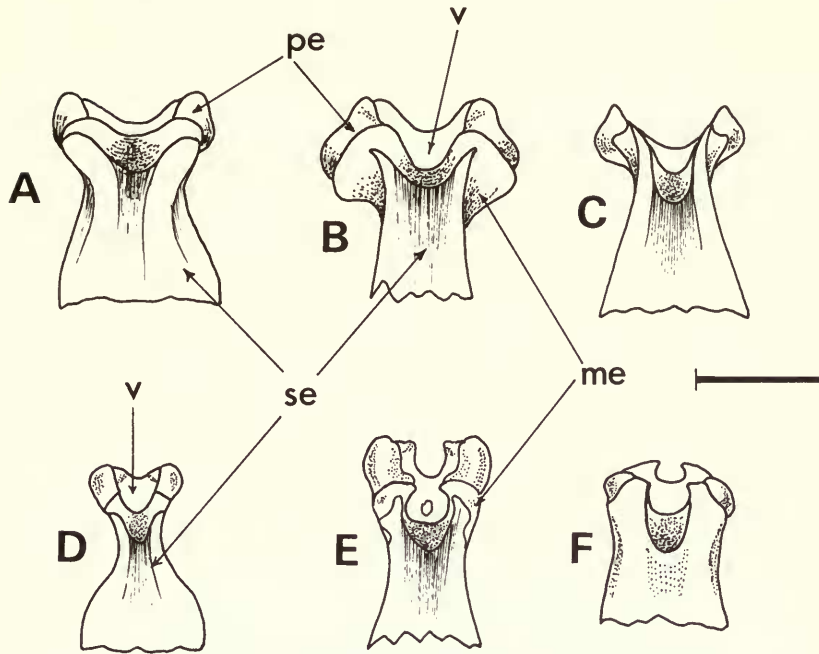


Fig. 3 Ethmoid region in dorsal view: A, *Neobola bottegi*; B, *Chelaethiops elongatus*; C, *C. bibie*; D, *Mesobola brevianalis*; E, *Rastrineobola argentea*; F, *Leptocypris niloticus*. me = mesethmoid; pe = preethmoid; se = supraethmoid; v = vomer. Scale = 1 mm.

*Myology* (Fig. 13). Section  $A_1$  of the *adductor mandibulae* muscle originates from the quadrate and preoperculum. There are two divisions of the section. (1), a triangular anterior part,  $A_{1ant}$ , which has an aponeurotic constriction below the anterior border of the eye and is bordered by the ligamentum primordium. This anterior segment continues along the maxilla as a narrow, parallel-fibred element and inserts below the outwardly curved palatine process of the maxilla; (2) a posterior part,  $A_{1post}$ , extending from the preoperculum to insert partly on the rictal tissue and partly onto the rim of the dentary coronoid process. Muscle  $A_2$  is thin and narrowly triangular, inserting into an aponeurosis medial to the anguloarticular; a small  $A_w$  section originates from the aponeurosis.

The *levator arcus palatini* is divided by the sphenotic process and inserts onto the lateral hyomandibular flange. The *dilatator operculi* is small and broadly triangular, originating from the sphenotic spur and inserting onto the small opercular process.

#### Pectoral girdle (Fig. 10)

The upright part of the cleithrum is short, the posterior lamellae lacking any central process; the tip of the horizontal limb extends to a point below the parasphenoid ascending process; the supracleithrum is short, articulating halfway along the cleithral limb; the coracoid is shallow with a fretted anterior border. There is no postcleithrum.

#### Vertebral column

The 1st vertebra has a flat articulatory face, it bears short lateral processes that are directed somewhat anteriorly. Centra 2 and 3 are fused and bear long, slightly posteriorly curved lateral processes. The caudal fin skeleton (Fig. 17A). has 6 hypurals, the 6th being minute. The fused preural and ural centra (PU1+U1) bear a small neural spine; the epural is long and slender; paired uroneurals are lacking. The parhypural bears a short but wide hypurapophysis. Dorsal and ventral procurrent rays are well-developed.

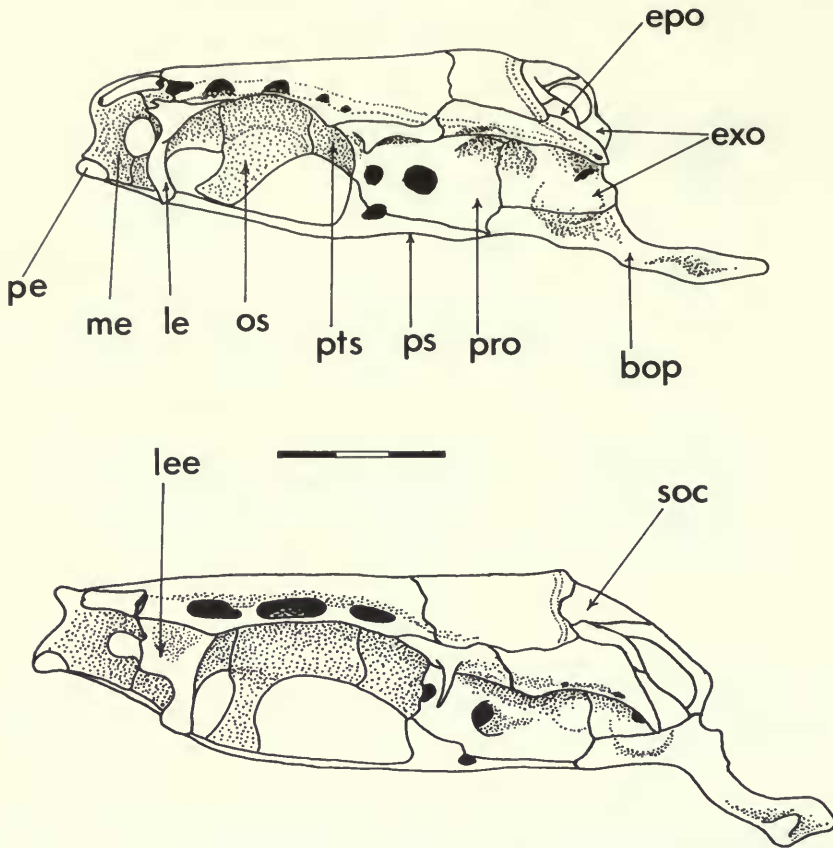


Fig. 4 Crania, in lateral view, (above) *Neobola bottegi* and (below) *Chelaethiops elongatus*. bop = basioccipital process; exo = exoccipital; lee = lateral ethmoid extension; os = orbitosphenoid; pro = prootic; ps = parasphenoid; pts = pterosphenoid; other abbreviations as in previous figs.

### Taxonomy

Three species are assigned to *Neobola*, *N. bottegi* Vinciguerra, 1895; from the Webei Shebéli and Omo rivers; *N. fluviatilis* (Whitehead), 1962 from the Athi and Tana rivers, Kenya and *N. stellae* (Worthington), 1932 from Lake Turkana, Kenya.

Whitehead (1962) separated *Neobola fluviatilis* from *N. bottegi* on its having fewer lateral line scales and a higher number of branched anal fin rays. However, I find there to be no substantial differences in these features. There are 37–40 lateral line scales in *N. bottegi* cf. 38–40 in *N. fluviatilis*. Anal fin rays range in *N. bottegi* from 14–18 (N14) cf. 19–21 (N18) in *N. fluviatilis*. Gill-raker counts similarly have a continuous range; 5–8 in *N. bottegi* (7 and 8 in specimens from the Webi Shebéli River and 5–6 in other specimens from other localities listed below) cf. 4–6 in *N. fluviatilis*. In both species there are 12 nasal lamellae on each half rosette. There are, however, differences in the morphology of the pectoral axial scale, it being smaller and more lobate in *N. fluviatilis* than in *N. bottegi*. Pharyngeal teeth in both species are in 2 rows, 4.3 or 5.3 in *N. bottegi* and 4.2 in *N. fluviatilis*. The total vertebral number for both species is 40 or 41 (4 Weberian + 14 abdominal + 21–22 caudal + the fused preural and ural centrum). It seems likely that *N. fluviatilis* is but the southern population of *N. bottegi*; further collections from northern Kenya and southern Ethiopia should help resolve this problem.

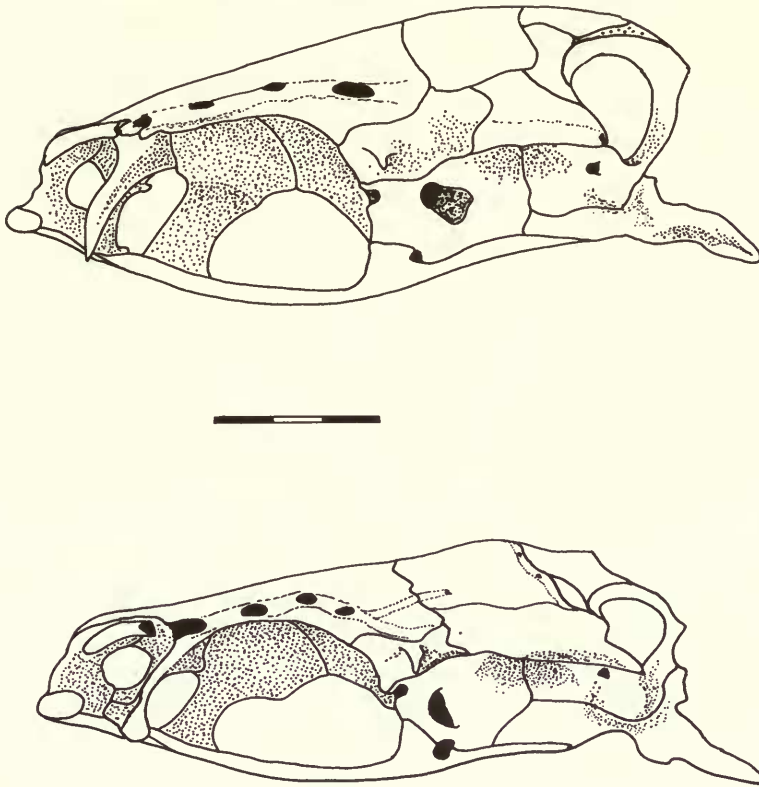


Fig. 5 Crania, in lateral view, (above) *Mesobola brevianalis* and (below) *Rastrineobola argentea*.

*Neobola stellae* (Worthington), 1932 is distinguished from *N. bottegi* and *N. fluviatilis* by its small size (maximum adult size measured, 25 mm SL), lower number of olfactory lamellae (10 on each half rosette), lower vertebral number (total, 37 or 38 cf. 40–41) and a small, bluntly triangular pectoral axial scale. There are 28–33 lateral line scales. Worthington (1932) gives a count of 34–37, but in fact none of the types have more than 34 lateral line scales even if one includes scales at the base of the caudal fin. Branched anal fin rays number 12–18. Pharyngeal teeth are in 2 rows, 4.2.

SPECIMENS EXAMINED. *Neobola bottegi*; 1902.11.7:22, Imi, Webi Shebeli; 1905.7.25:94–5, Modjo R.; 1905.7.25:110–112, Wabbi R.; 1905.7.25:106–9, Iraro R.; 1950.11.25:5–6, Webi Shebeli; 1982.5.17:9–14, Webi Shebeli. *Neobola fluviatilis*; 1961.5.3:1 (holotype); 2–6 (paratypes), Athi R. near Kithimani; 1966.7.5:29–42, Athi R. at Yalta; 1966.8.25:6, Tana R. *Neobola stellae*; 1932.6.13:57–65 (syntypes); 1932.6.13:47–56, all labelled 'Lake Rudolf'; 1973.8.6:65–76, Loiengalani; 1981.12.17:2488–2587, Lodge Spit; 1981.12.17:2173–82, Ferguson's Gulf, Lake Turkana.

### **CHELAETHIOPS** Boulenger, 1899

*Chelaethiops* is characterized by its pointed snout and long, shallow jaws, the articulation of the lower jaw extending posterior to the centre of the eye, a dorsally channelled broad to narrow supraethmoid, laterally opening frontal pores, 16–26 olfactory lamellae on each half rosette, few (5) to many (18) gill-rakers on 1st ceratobranchial, elongate pectoral axial scales, pharyngeal teeth long, recurved in three rows, 5.3.2. Scales with 7–9 widely

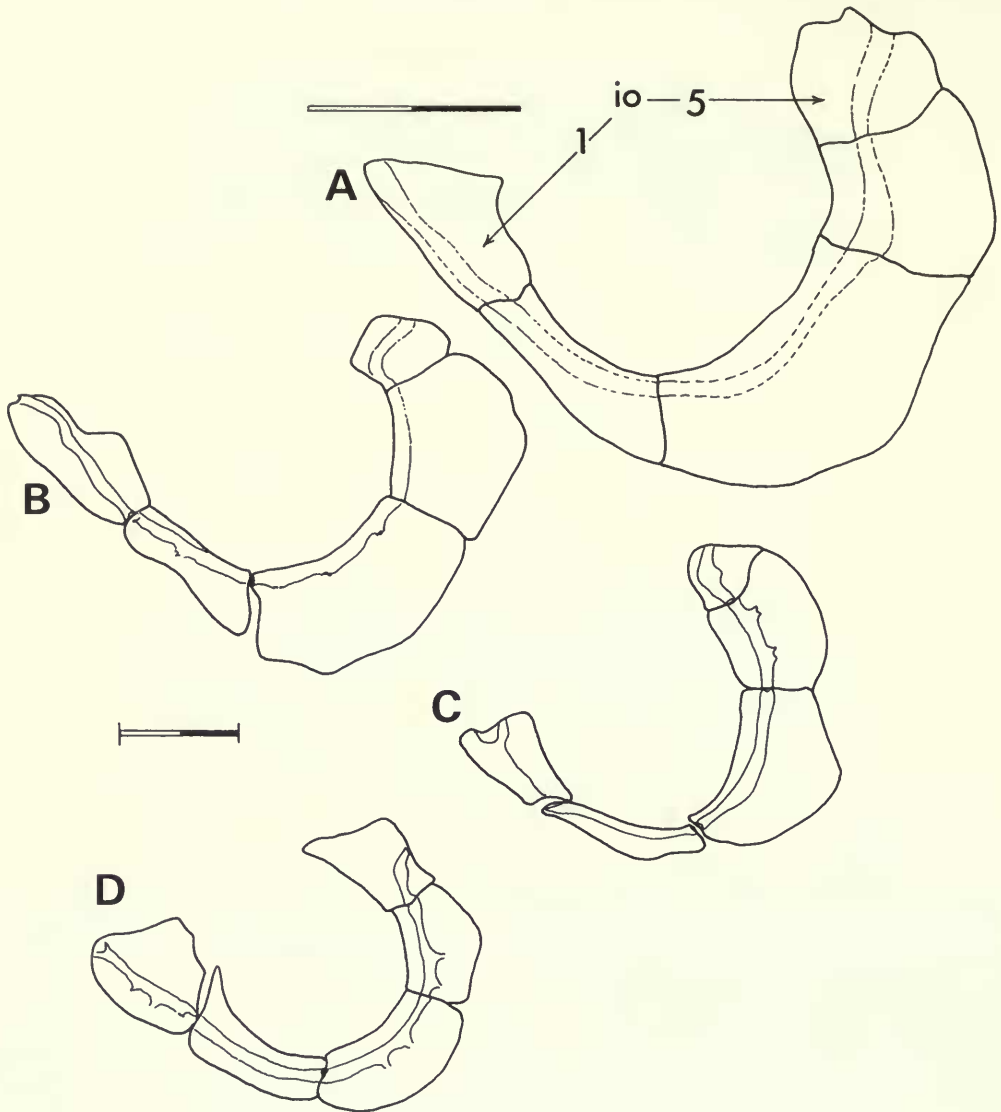


Fig. 6 Infraorbital bones: A, *Neobola bottegi*; B, *Chelaethiops bibie*; C, *Mesobola brevianalis*; D, *Rastrineobola argentea*.

spaced radii, 36–42 lateral line scales; the lateral line gently decurved anteriorly and with a pronounced curve above the pelvic fin base, often with a wave-like irregularity along the caudal peduncle; swimbladder has short anterior and posterior chambers, the posterior extending to above the pelvic fin (exceptionally, long in *C. minutus*, extending to above the anal fin origin).

CONTAINED SPECIES. *Chelaethiops elongatus*, *C. bibie*, *C. congicus*, *C. minutus* and *C. rukwaensis*.

### Cranial anatomy

*Osteology.* The *ethmoid bloc* is short and deep, its anterior border varies interspecifically from shallow to deeply indented (Fig. 3B & C). The lateral edges of the supraethmoid are



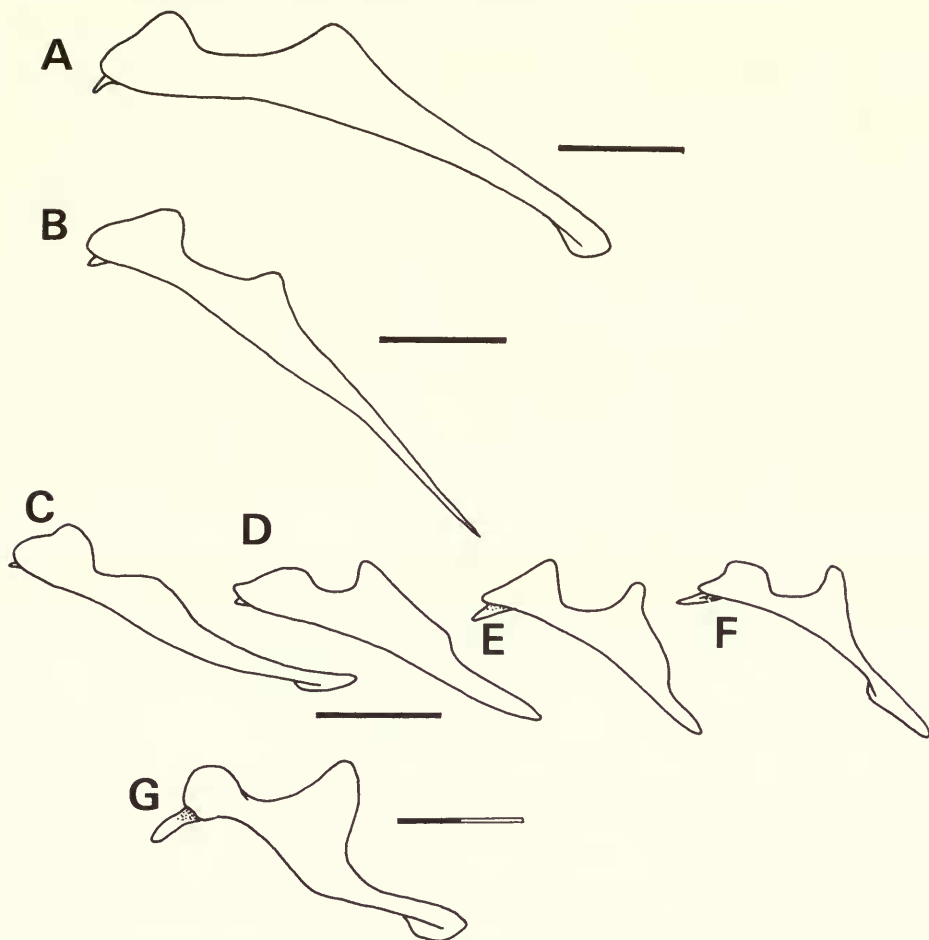


Fig. 7 Maxillae: A, *Neobola bottegi*; B, *Chelaethiops bibie*; C, *Neobola stellae*; D, *Mesobola spinifer*; E, *M. bredoi*; F, *M. brevianalis*; G, *Rasterineobola argentea*. Scales in mm.

raised and the width of the dorsal channel is also interspecifically variable. The mesethmoid is deep, its arms widely divergent, abutting on large preethmoids. The vomer floors the mesethmoidal indentation. As in *Neobola* the lateral ethmoid has an anterior extension of its dorso-lateral wall (lee, Fig. 4).

The *frontals* are narrower than those of other neobolines, the sensory canal is more highly developed, and there are 4 large, conspicuous pores all of which open laterally. The *nasal* is large and reduced to the sensory canal tube with one dorsal pore or none.

The *infraorbitals* more closely resemble those of *Neobola* than any other neoboline genus, both in their width and orbital configuration. The sensory canal, however, runs along the orbital margin of the bones and the 4th infraorbital is longer than in *Neobola* (Fig. 6B).

The *neurocranium* is similar to that of *Neobola* except that the sphenotic has a ventrally directed process, and there is a ventral opening between the basioccipital and the parasphenoid.

The *jaws* are long (Figs 7 & 8); the maxilla has a low, long palatine process and the bone terminates in a spine-like tip. The upper jaw bones are longer and more slender than those of any neoboline genus. The lower jaw closely resembles that of *Neobola* except that the symphyseal process of the dentary is more prominent and the coronoid process is lower and backwardly sloped at a shallower angle.

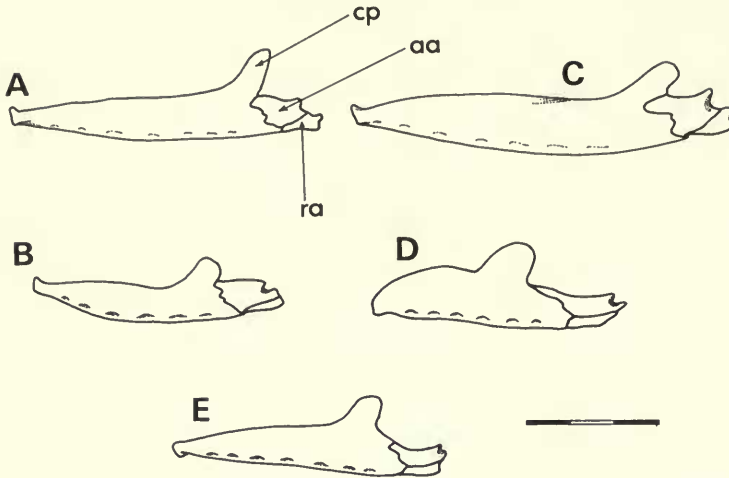


Fig. 8 Lower jaw bones: A, *Neobola bottegi*; B, *Mesobola brevianalis*; C, *Chelaethiops elongatus*; D, *Rastrineobola argentea*; E, *Leptocypris niloticus*. aa = anguloarticular; cp = coronoid process; ra = retroarticular.

The *suspensorial bones* are like those of *Neobola* except that the hyomandibula has a pronounced concavity to its lower anterior border and only a slight indentation separates the articulatory condyles. The posterior condyle is shaped into a long, triangular process. The palatine, ecto-, ento- and metapterygoids are all longer than those elements in *Neobola* and the metapterygoid has only a slight anterior dorsal process (cf. Figs 9A & B).

The *operculum* has a rounded dorsal border and a strongly attenuated, rather triangular lower border (Fig. 9B).

*Myology* (Fig. 13). Muscle *adductor mandibulae*  $A_1$  is divided into anterior and posterior segments as in *Neobola*. The anterior part  $A_{1,ant}$ , extends from the quadrate to insert below the maxillary cleft. The segment contains an aponeurotic constriction below the anterior border of the eye. The aponeurosis is divided so that the orbital part serves as the site of the attachment for the fibres from the lower part of the muscle, and the outer division is continuous with the *ligamentum primordium* and serves as the site of attachment for the fibres of the anterior part of that muscle. The posterior segment of muscle  $A_1$ ,  $A_{1,post}$ , originates from the preoperculum and inserts on to the coronoid process of the dentary and on the rictal tissue. There is no  $A_w$  section of the *adductor mandibulae*. The configuration of other jaw and suspensorial muscles are as described for *Neobola*.

#### Pectoral girdle (Fig. 10C)

The pectoral girdle resembles that of *Neobola*; the coracoid is deeper than in other neobolines and has a markedly fretted antero-ventral margin. There is no postcleithrum.

#### Vertebral column (Fig. 12)

The anterior face of the 1st centrum is rounded (cf. flat in *Neobola*), the centrum bears long lateral processes, the distal tips of which underlie the processes of the fused 2nd and 3rd centra. The lateral processes of the fused centra are curved posteriorly, their distal tips reaching to a level with the articulation of the 3rd and 4th centra. The neural complex is upright, the 4th neural spine sloped backward at a low angle (Fig. 12). A large plate-like supraneural, possibly two fused supraneurals, overlies the 4th neural spine and extends backwards to above the 5th; this is followed by 6 or more elements varying in shape from triangular plates to thin rods. The caudal skeleton differs from that of *Neobola* in elongation of the 6th hypural, the neural spine on the fused preural-ural centrum and the hypurapophysis (Fig. 17B).

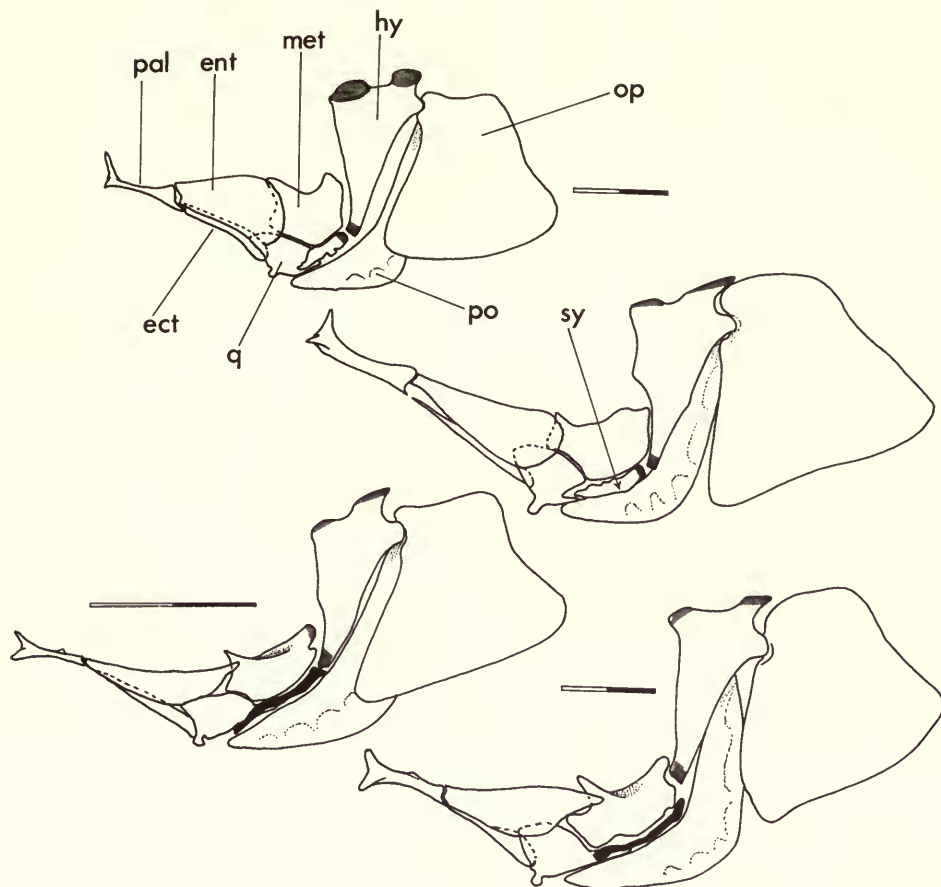


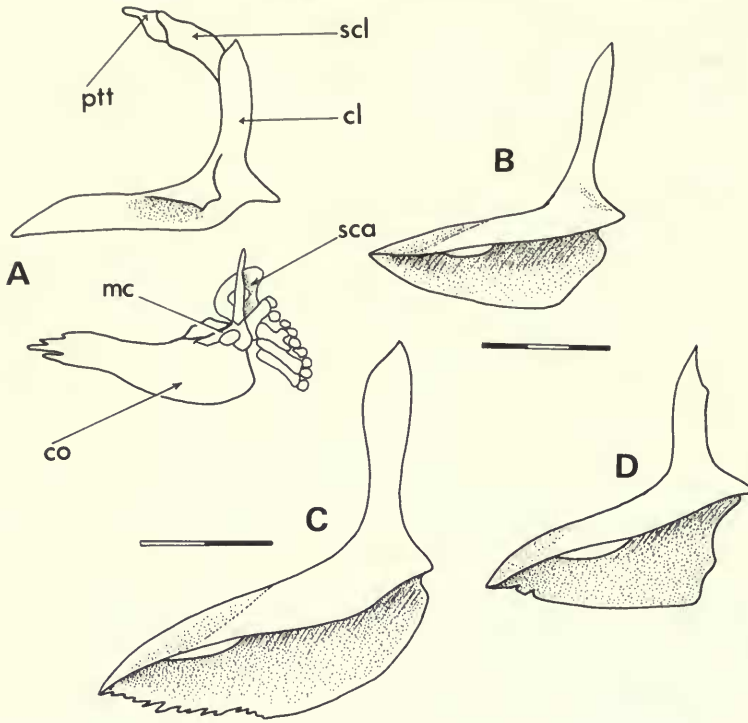
Fig. 9 Suspensoria in medial view: A, *Neobola bottegi*; B, *Chelaethiops elongatus*; C, *Mesobola brevianalis*; D, *Rastrineobola argentea*. ect = ectopterygoid; ent = entopterygoid; hy = hyomandibula; met = metapterygoid; op = operculum; pal = palatine; po = preoperculum; q = quadrate; sy = symplectic. In *Mesobola* and *Rastrineobola*, the symplectic is shown in solid black.

### Taxonomy

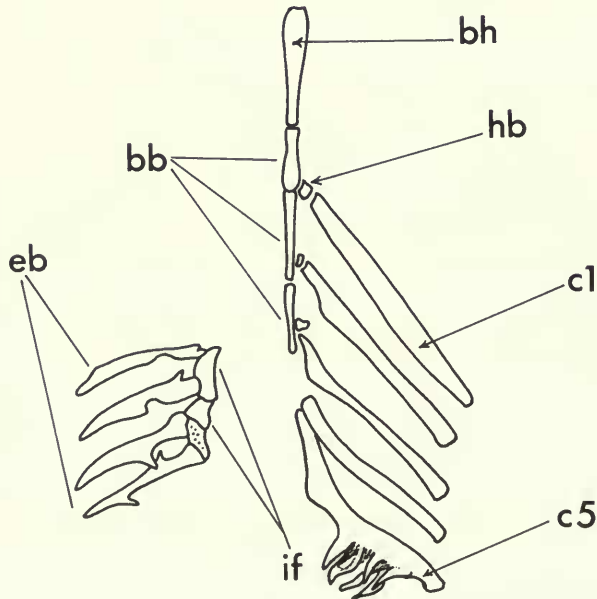
Boulenger (1911) included two species in *Chelaethiops*, viz: *elongatus* and *bibie*. Since then only one other species has been described, *C. katangae* Poll, 1948. Howes (1980) assigned three other species to the genus, *Engraulicypris congicus* Nichols & Griscom, 1917, *Neobola minuta* Boulenger, 1906, and *Engraulicypris rukwaensis* Ricardo, 1939.

*Chelaethiops elongatus* Boulenger, 1899, is characterized by its long and pointed snout and upwardly inclined head (Fig. 19B); a distinct mandibular symphyseal notch; 16–17 olfactory lamellae on each half rosette; 5 short gill-rakers on the 1st ceratobranchial; 16–17 branched anal fin rays; 36–38 lateral line scales; axial pectoral scale 30–33% pectoral fin length (Fig. 18C); pectoral fin extending to the origin of the pelvic fin; lower part of posterior opercular border attenuated; pharyngeal teeth in 3 rows, 5.3.2; vertebrae 38 or 39 (4+11–12+21–22+1, see p. 156 for method of counting). Distribution of the species is the Zaire drainage.

*Chelaethiops bibie* (Joannis), 1835, is characterized by its narrow supraethmoid with well-developed dorsal channel (Fig. 3C). The snout is pointed but more strongly curved than in *C. elongatus* and there is a prominent ridge above the eye (Fig. 19A). There are 12–13 olfactory lamellae on each half rosette; 9 or 10 short gill-rakers on 1st ceratobranchial; 16–17



**Fig. 10** Pectoral girdles: A, *Neobola bottegi* (medial view of disarticulated girdle); B, *Mesobola brevianalis*; C, *Chelaethiops elongatus*; D, *Rastrineobola argentea* (medial views). cl = cleithrum; co = coracoid; mc = mesocoracoid; sca = scaphium; scl = supracleithrum; ptt = posttemporal.



**Fig. 11** Branchial arches of *Mesobola brevianalis*. bb = basibranchials; bh = basihyal; C1 - 5 = ceratobranchials; eb = epibranchials; hb = hypobranchials; if = infrapharyngobranchials.

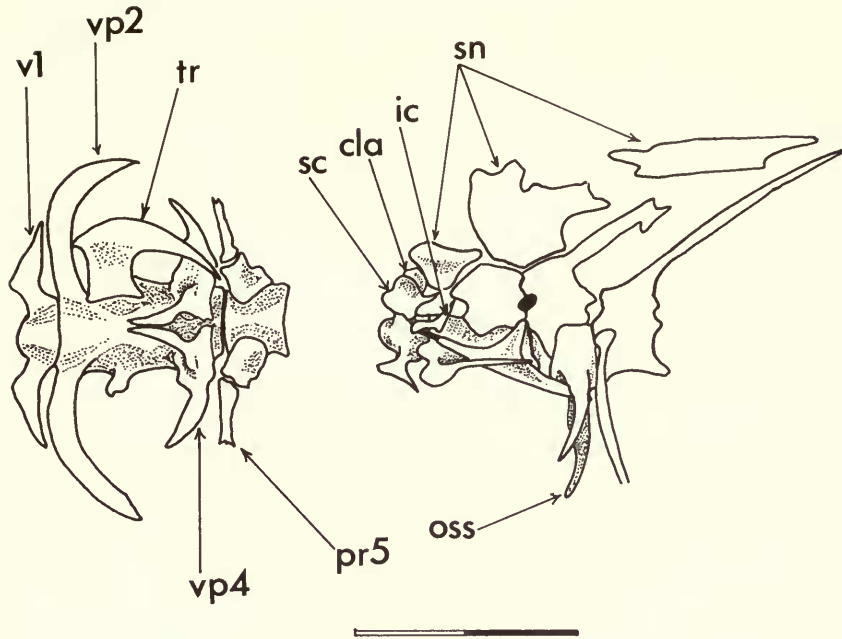


Fig. 12 Anterior vertebrae, in ventral and lateral views, of *Chelaethiops bibie*. cla=claustrum; ic=intercalarium; oss=ossa suspensorium; pr=pleural rib; sc=scaphium; sn=supraneurals; tr=tripus; v=vertebrae; vp=lateral vertebral process.

branched anal fin rays (rarely 14 or 18); 36–38 lateral line scales; the lateral line usually more irregular and sinuous than that of *C. elongatus*; axial pectoral scale about 20% of pectoral fin length (Fig. 18E); pectoral fin extending to beyond the origin of the pelvic fin; lower part of the posterior opercular border attenuated; pharyngeal teeth in three rows, variants are 5.3.1. or 4.3.1; vertebrae 36–40 (4+11–13+19–22+1).

Daget (1954) described a subspecies from the Upper Niger which he named as *C. elongatus brevianalis*. Blache & Miton (1960) decided that Daget's taxon represented a species, which comprised two subspecies, *C.b. brevianalis* and *C.b. lerei* from the Mayo Kebbi. It would seem, however, that Daget did not consider *C. bibie* as he makes no mention of the species in his description. There is no difference between *C. bibie* and Daget's description of *C. elongatus brevianalis*. It may well be that Blache & Miton's (1960) taxon from the Mayo Kebbi represents a subspecies, or morphologically distinct population, but this fact has yet to be established. There are differences in vertebral counts between Nilotic *C. bibie* and those from Ghana as follow: Nilotic specimens; 12 or 13 abdominal and 22 caudal, Ghanaian specimens; 11 or 12 abdominal and 19 or 20 caudal. *Chelaethiops bibie* occurs in the Nile (including Lake Turkana), Niger (eastern limit uncertain) and Volta.

*Chelaethiops minutus* (Boulenger), 1906, is characterized by its narrow supraethmoid with well-developed dorsal channel; long and downwardly curved snout, its tip extending beyond that of the lower jaw (Fig. 19E); a prominent frontal ridge above the orbit; 25–27 olfactory lamellae on each half rosette; 17 or 18 long gill-rakers on the 1st ceratobranchial; 18–21 branched anal fin rays; 39–42 lateral line scales; axial pectoral scale 22–25% pectoral fin length (Fig. 18G); pectoral fin not reaching beyond the origin of the pelvic fin; posterior border of the operculum rounded; pharyngeal teeth in 3 rows, 5.3.2; vertebrae 39 or 40 (4+12–13+22–23+1).

This species differs from other *Chelaethiops* in gill-raker length and number, an elongate posterior chamber of the swimbladder extending to, or just beyond, the anal fin origin and

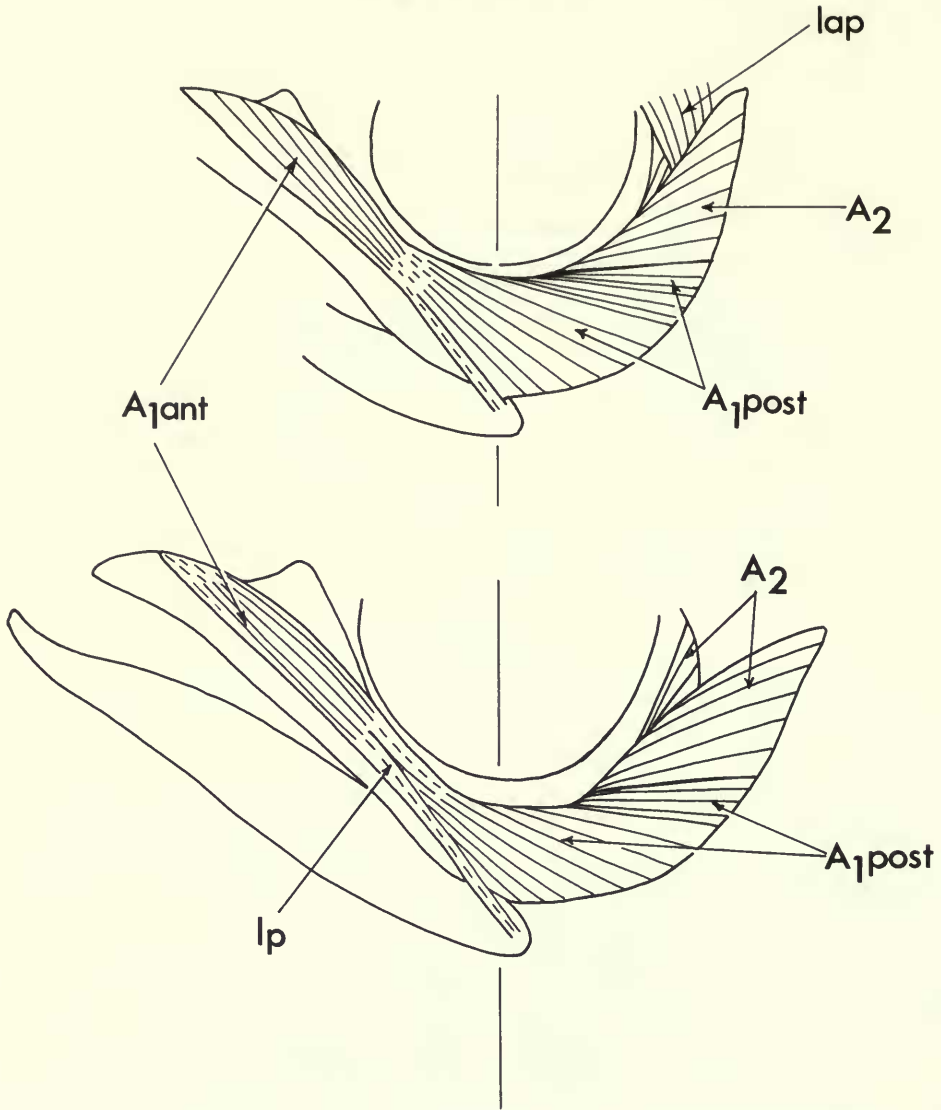


Fig. 13 Jaw muscles of (above) *Neobola bottegi* and (below) *Chelaethiops elongatus*. A = divisions of the adductor mandibulae muscle; lp = ligamentum primordium; lap = levator arcus palatini; the vertical line marks the orbital centre.

the articulation of the anterior 3 or 4 supraneural bones. It is endemic to Lake Tanganyika (see Poll, 1953).

*Chelaethiops congicus* (Nichols & Griscom), 1917, is characterized by its short and blunt snout (Fig. 19C); broad supraethmoid with shallow dorsal channel; 12–15 olfactory lamellae in each half rosette; 5–6 short gill-rakers on the 1st ceratobranchial; 16–18 branched anal fin rays; 38–42 lateral line scales; axial pectoral scale 30–33% pectoral fin length (Fig. 18F); pectoral fin extending to the origin of the pelvic fin; upper part of posterior opercular border concave; pharyngeal teeth in 3 rows, 5.4.1 or 5.3.1; vertebrae 41 (4 + 14 + 22 + 1).

It appears that although authors have cited *C. congicus* in their comparative analyses, none has actually examined the type specimens (Poll, 1945; Whitehead, 1962; Ricardo,

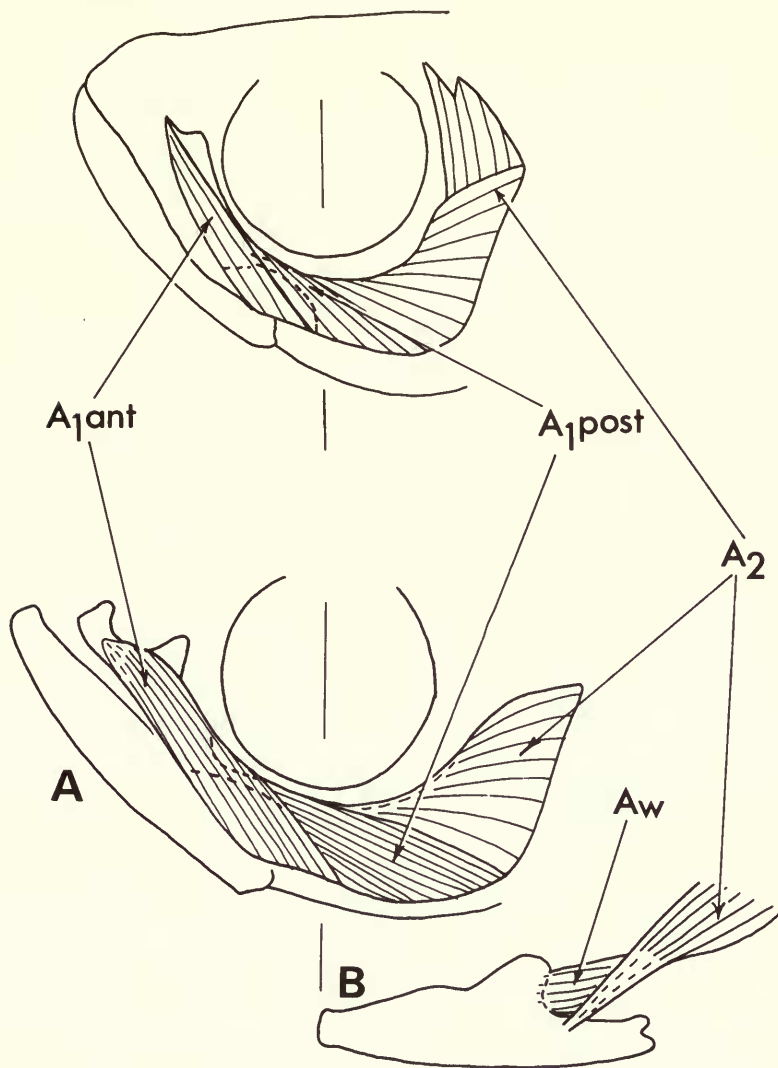


Fig. 14 Jaw muscles of (above) *Mesobola brevianalis* and (below) *Rastrineobola argentea*. A, lateral and B, medial views.

1939). Poll (1948) described *Chelaethiops katangae* from the Lufira, Zaire. Poll did not, however, compare his specimens with *C. congicus* but only with *C. elongatus* and *C. bibie*. I find the holotype of *C. congicus* to be closely similar to the syntypes of *C. katangae* in all morphological aspects and consider *C. katangae* to be a synonym of *C. congicus*. The distribution of *C. congicus* is the Zaire basin.

*Chelaethiops rukwaensis* (Ricardo), 1939, is characterized by its narrow supraethmoid with well-developed dorsal channel; pointed and curved snout (Fig. 19D); 16–17 olfactory lamellae in each half rosette; 5–6 short gill-rakers on the 1st ceratobranchial; 15–17 branched anal fin rays; 36–38 lateral scales; axial pectoral scale with wavy border (Fig. 18F), 20–25% pectoral fin length; pectoral fin extending to the origin of the pelvic fin; upper posterior border of the operculum shallowly concave, lower border slightly attenuated; pharyngeal teeth in 3 rows, 5.3.1; vertebrae 38–40 (4 + 14 – 16 + 19 + 1).

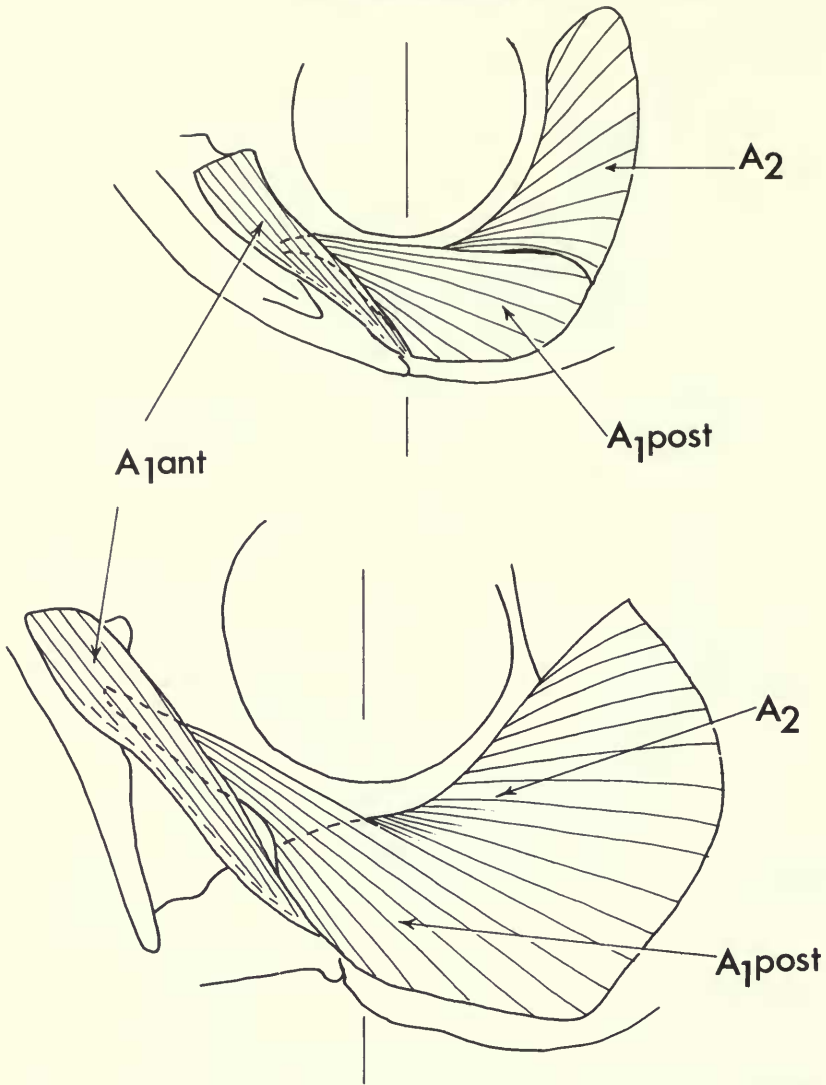


Fig. 15 Jaw muscles of (above) *Leptocypris niloticus* and (below) *Raiamas senegalensis*.

Ricardo (1939) described, from Lake Rukwa, a subspecies of *Chelaethiops congicus*, commenting: 'It is . . . thought best to regard the examples from L. Rukwa as a new subspecies of *E. congicus* in order to show that they do differ from all forms previously known and that they are more closely related to the *Engraulicypris* in L. Tanganyika and the Congo than to any of the species found in other lakes or rivers.'

From this statement it would seem that Ricardo was regarding the subspecies as a convenience category to demonstrate her opinion of relationship. The comparative material from Lake Tanganyika and the Congo used by Ricardo is in fact composite. The specimens from the Congo are those included herein under *C. congicus*, but those from Lake Tanganyika differ in morphometric and other characters and, in these respects, are closer to the samples from Lake Rukwa. As with the Lake Rukwa specimens, the Lake Tanganyika sample has a pectoral axial scale length of 20–25% the pectoral length, cf. 30–33% in *C.*



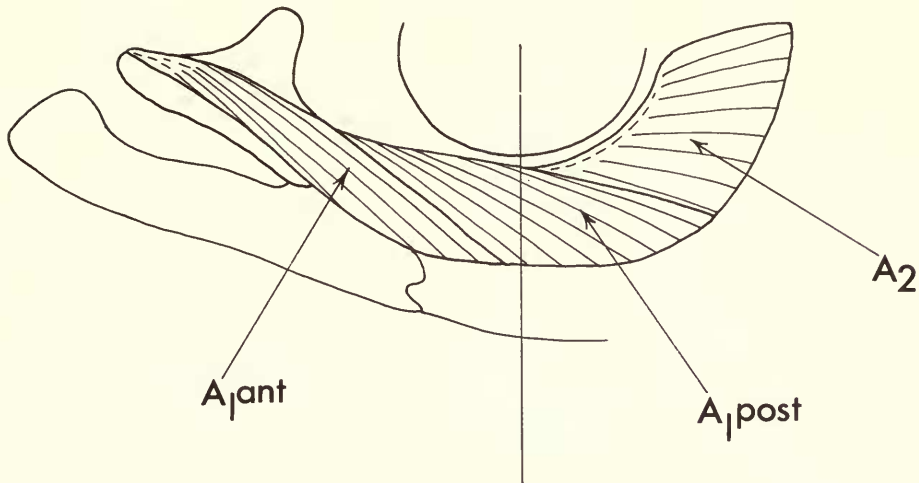


Fig. 16 Jaw muscles of *Engraulicypris sardella*.

*congicus*, 16–18 olfactory lamellae, cf. 12–15 in *C. congicus*, and 36–38 lateral line scales, cf. 38–42 in *C. congicus*.

There is an added difficulty concerning the exact provenance of the 'Lake Tanganyika' sample of *C. rukwaensis*. Neither Poll (1953) nor Brichard (1978) in their respective accounts of Lake Tanganyika fishes record any species of *Chelaethiops* (their *Engraulicypris*) other than *C. minutus*. The record of Lake Tanganyika *C. congicus* given by Ricardo (1939) is based on the material collected by Christy. No more precise locality is available than 'L. Tanganyika' and it may well be that the specimens were collected in the environs of the lake.

Howes (1980) noted that *C. rukwaensis* was most closely related to an undescribed taxon from Lake Tanganyika. The taxon is the 'L. Tanganyika' sample discussed above. The status of the taxon is difficult to determine on the basis of such a small sample (55 specimens) and with imprecise locality data. It is further complicated by specimens from the Luiche river, Malagarasi system, having characters intermediate between the *C. rukwaensis* and *C. congicus* (*viz.*: 38 lateral line scales, 14 branched anal fin rays and 12 olfactory lamellae on each half rosette). The 'L. Tanganyika'-Malagarasi forms may eventually prove to be a morphologically distinct local population (or subspecies) but for the present my study material is identified only as '*Chelaethiops rukwaensis*'.

**SPECIMENS EXAMINED.** *Chelaethiops elongatus*: 1901.12.26:31, Banzyville Ubanghi; 1912.12.6:9–10, Dungu, Uelle; 1919.9.10.241–2, Avakubi, Ituri; 1920.7.12:39–40, Banghi; 1975.6.20:308–40, 34–43, 344–47, Lualaba; 348–49, Ituri Bridge; MRAC 85848–947, Ankoro, Lualaba.

*Chelaethiops bibie*. Nile: 1904.9.26:22–23, Kalioub, north of Cairo; 1907.13.2:1513–9, near Luxor; 1520–23, between Luxor and Asswan; 1524, Asswan; 1525, Kermeh, Nubia; 1526–1626, Omdurman; 1627, White Nile; 1628–31, Lake No; 1632–51, 52–53, Gondokoro; 1913.11.11:5–7; Khor Barboy; 1924.5.21:1–5, near Cairo; 1981.2.17:1314–1358, Tode-nyang, L. Turkana; 1369–1431, Morago R., Turkana; 2378–2427, west shore, L. Turkana; 2428–2437, Ferguson's Gulf, L. Turkana. **West Africa**: 1935.5.29:9–18, Kaduna, Nigeria; 1969.11.14:109–23, Volta, Ghana; 1974.1.2:185, Black Volta; 1982.4.13:783–93, Bahindi, Nigeria; 794–797, Sokoto R., 821–830, Sokoto-Rima floodplain; 799–811, 812–820, Rima R., N. Nigeria.

*Chelaethiops minutus*: 1906.9.8:55–60 (syntypes), Mbeté (14–24 mm SL); 1955.12.20:1021–1029, L. Tanganyika (54–66 mm SL); 1982.9.24:61–66, Kigoma (67.5–86.5 mm SL).

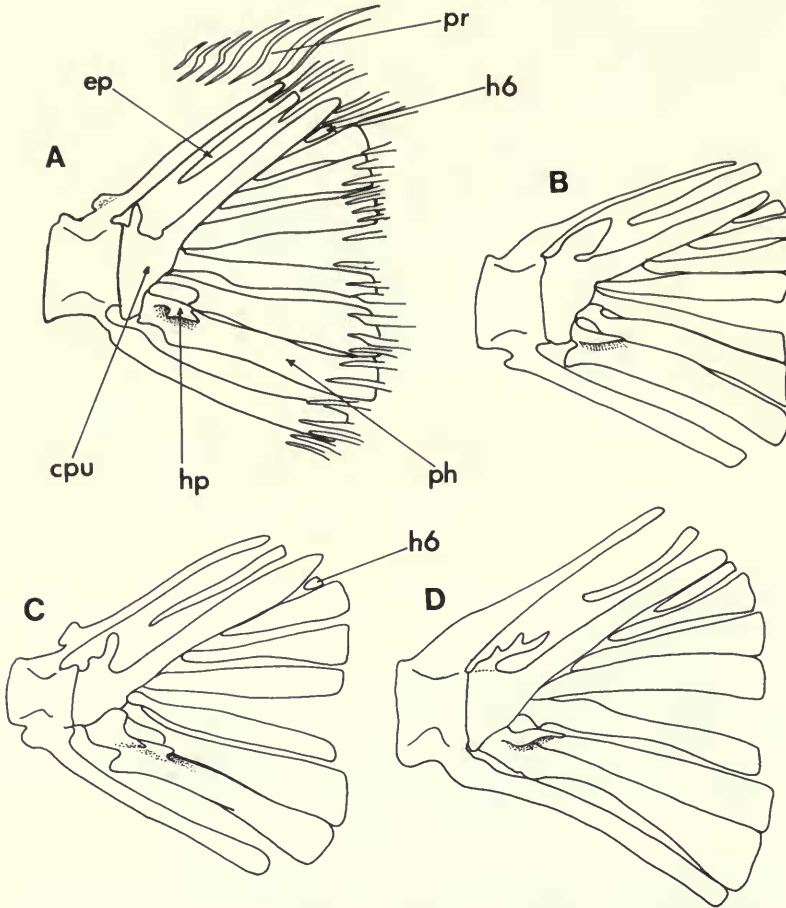


Fig. 17 Caudal fin skeletons: A, *Neobola bottegi*; B, *Chelaethiops elongatus*; C, *Mesobola brevipennis*; D, *Rastrineobola argentea*. cpu = fused preural-ural centrum; ep = epural; h6 = 6th hypural; hp = hypurapophysis; ph = parhypural; pr = procurent rays.

*Chelaethiops congicus*; AMNH 6295 (holotype), Poko, Ubangi; MRAC 78108-9 (syntypes of *C. katangae*), Kafila, Lufira; BMNH 1919.9.10:238, Avakubi, Ituri; 1919.9.10:239, Busabangi, Lindi; 1902.4.14:47-8, Lindi R.; 1907.4.30:42, Atuwimi R.; 1909.7.9:62, Bumba (Boumba) R., Assobam, S. Cameroon; 1975.6.20:350-402, Lufira R.

*Chelaethiops rukwaensis*; 1942.12.31.:191-210 (syntypes), Lake Rukwa; 1936.6.15:547-67, 'L. Tanganyika'; 1969.1.31:49-105, Lake Rukwa; 1971.6.22:137-138, Luiche R., Malagarasi system.

### MESOBOLA gen. nov.

TYPE SPECIES. *Engraulicypris brevipennis* Boulenger, 1908, *Ann. Natal Mus.* 1: 231

This genus is uniquely defined by its cranial, jaw bone and jaw muscle morphology. At the same time it can be included with *Neobola*, *Chelaethiops* and *Rastrineobola* on the basis of those synapomorphies defining the neoboline group (p. 177). *Mesobola* is characterized by a narrow, dorsally channelled supraethmoid; vomer forming a floor to the ethmoid indentation; pre-ethmoids directed rostrad; nasal without dorsal pores; frontal canal with 4 or 5 pores; narrow, triangular metapterygoid process; symplectic elongate with expanded tips;

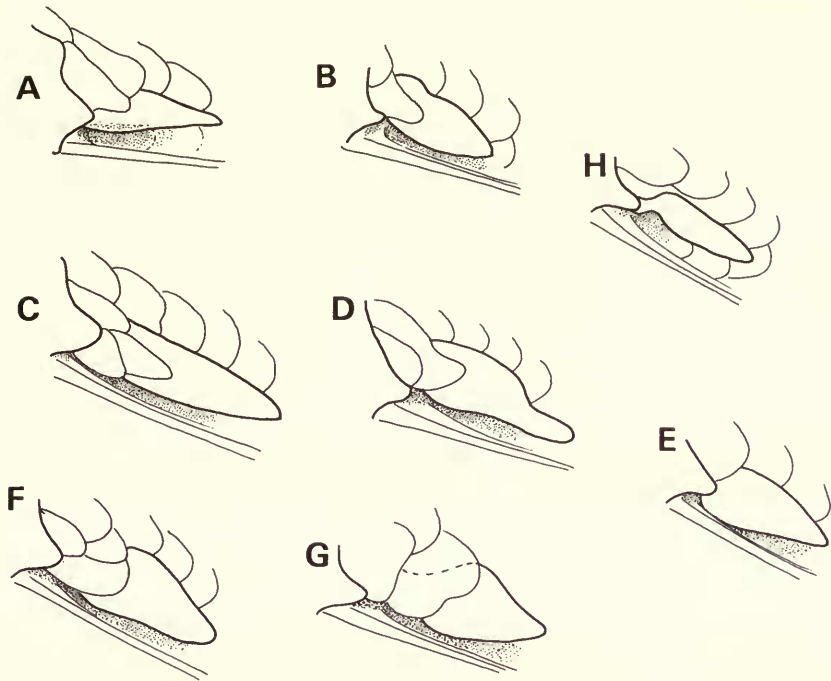


Fig. 18 Pectoral axial scales: A, *Neobola bottegi*; B, *Neobola stellae*; C, *Chelaethiops elongatus*; D, *C. rukwaensis*; E, *C. bibie*; F, *C. congicus*; G, *C. minutus*.

8–10 olfactory lamellae on each half rosette; pectoral axial scale absent; pharyngeal teeth in 3 rows; swimbladder with long anterior and posterior chambers, the posterior curved downward and terminating above the anus.

CONTAINED SPECIES. *M. brevianalis*, *M. spinifer*, *M. bredoi* and *M. moeruensis*.

### Cranial anatomy

**Osteology.** The most characteristic feature of the cranium is the morphology of the ethmoid region (Fig. 2D). The *ethmoid bloc* is hour-glass shaped, the supraethmoid with a deep anterior notch, its lateral walls lamellate and forming a deep channel posterior to the notch. The mesethmoid has a V-shaped anterior indentation, the preethmoids being situated on the tips of the mesethmoid arms and thus considerably extending the depth of the indentation. The vomer floors the notch and where it meets the preethmoids there is a thickening of the bone, thus forming what appears to be medial processes of the preethmoids. In some specimens there is a small vomerine foramen. The lateral ethmoid margin curves antero-ventrally and lacks the dorsal lamellae present in *Neobola* and *Chelaethiops*.

The frontal canal (Fig. 2C) lies close to the edge of that bone and has 4–5 pores. The size and position of the canal pores is interspecifically variable, but the posterior pore always opens laterally. The *nasal* is large, lacking dorsal pores. The *cranial roof* is convex in the area of the fronto-parietal suture; in all other neoboline genera the roof is flat.

The *infraorbitals* (Fig. 6C) are shallow, as in *Rastrineobola* (cf. deep in *Neobola* and *Chelaethiops*). The infraorbital canal runs along the ventral part of the 1st bone, the orbital border of the 2nd and through the centres of the 3rd, 4th and 5th infraorbitals.

The *orbitosphenoids* are connected to the parasphenoid *via* a deep, narrow septum. The anterior trigemino-facialis foramen indents the border of the *prootic* and there is a long lateral commissure (Fig. 5). There is a small foramen between the parasphenoid and basioccipital.

The *jaws* are long (Figs 7 & 8); the palatine process of the maxilla varies interspecifically from being low and long, to high and triangular in shape (see p. 180 & Figs 7D–F). The articulation of the dentary with the quadrate is below the centre of the orbit. The dentary is rather deep with a convex dorsal border and a backwardly sloped coronoid process. The anguloarticular has a long, almost horizontal dorsal border.

The *suspensorium* (Fig. 9C). The hyomandibula is narrow with a straight anterior border. The dorsal border is sloped so that the anterior articulatory condyle is at a level lower than that of the posterior condyle. The ento- and metapterygoids are deeper than those of other genera. The entopterygoid is long with a slightly concave dorsal border; the metapterygoid has a narrow, triangular anterior process directed mesad. The most noticeable feature of the suspensorial elements is the length and shape of the symplectic. The bone is excessively elongate with expanded tips where it contacts the quadrate and the hyomandibula.

*Branchial arches* (Fig. 11). The ceratobranchials bear 7–12 long gill-rakers, pharyngeal teeth are arranged in 3 rows with interspecific variation of 4.2.1, 4.3.1 and 5.3.2.

The *operculum* has a concave upper posterior border and an attenuated lower part (Fig. 9C).

*Myology* (Fig. 14). As in *Neobola* and *Chelaethiops*, section  $A_1$  of the *adductor mandibulae* muscle is divided, but  $A_{1,ant}$  lacks the aponeurotic constriction present in those two genera and extends from the quadrate to insert below the anterior cleft of the maxilla. Muscle  $A_{1,post}$  extends from the lower limb of the preoperculum to insert partly on the coronoid process of the dentary and partly, *via* a long tendon, into the fascia of  $A_{1,ant}$ . Other muscles are arranged as in *Neobola*.

#### Pectoral girdle (Fig. 10)

The upright part of the cleithrum is narrower than in *Neobola* and more closely resembles that of *Chelaethiops* in shape; the coracoid is deep and its posterior border forms a sharp angle with the ventral border. There is no postcleithrum.

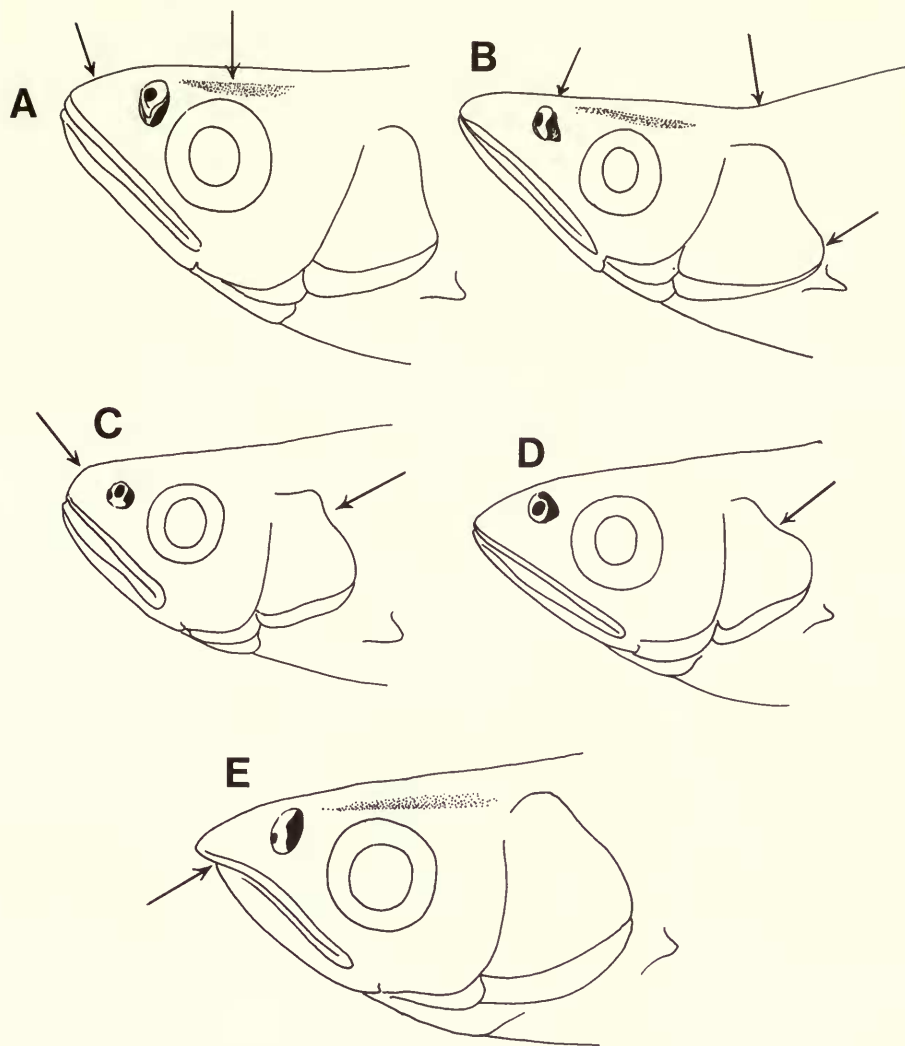
#### Vertebral column

The 1st vertebra has a flat anterior face, and short, blunt lateral processes. The 2nd and 3rd centra are fused, bearing long, lateral processes with posteriorly curved tips. The caudal fin skeleton closely resembles that of *Neobola* in having a small 6th hypural and reduced spine on the fused ural centrum, and short hypurapophysis (Fig. 17C). There are no paired uroneurals. Dorsal and ventral procurrent rays are well-developed.

#### Taxonomy

*Mesobola brevianalis* (Boulenger), 1908, is characterized by a maxilla with a high, narrowly triangular mid-lateral (palatine) ascending process (Fig. 7F); 10 olfactory lamellae on each half rosette; absence of pectoral axial scales; 12–15 branched anal fin rays (12 in the type specimen, 14–15 in others); 9–12 gill-rakers on 1st ceratobranchial; 48–50 lateral line scales, the lateral line with a pronounced and abrupt downward curve over the pectoral fin, and another at the caudal fin base; pectoral fin reaching to origin of the pelvic; pharyngeal teeth in 3 rows, interspecific variation, 4.2.1–5.3.2; swimbladder with long anterior and posterior chambers, the posterior curving downward and terminating above the anus; vertebrae 39 or 40 (40 + 13 – 14 + 20 – 22 + 1).

Jubb (1967) gives a description, synonymy and distribution for the species. Bell-Cross (1956a) records *M. brevianalis* from the Kabompo river and an 'isolated' example from Fort Rosebery, off the Luapula river. Jubb (1967) refers to *M. brevianalis* from the Cunene river, although this species is not listed by Bell-Cross (1965b) in his check-list of the fishes of that river. The species is recorded from Zambia, Zimbabwe, Transvaal and Natal. On the western side of South Africa, it occurs below the Aughrabies Falls of the Orange river (Jubb, 1967: 127).

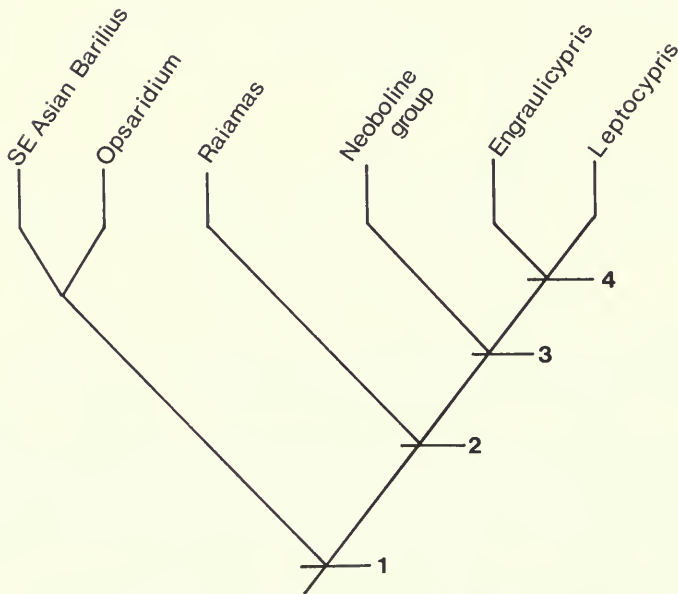
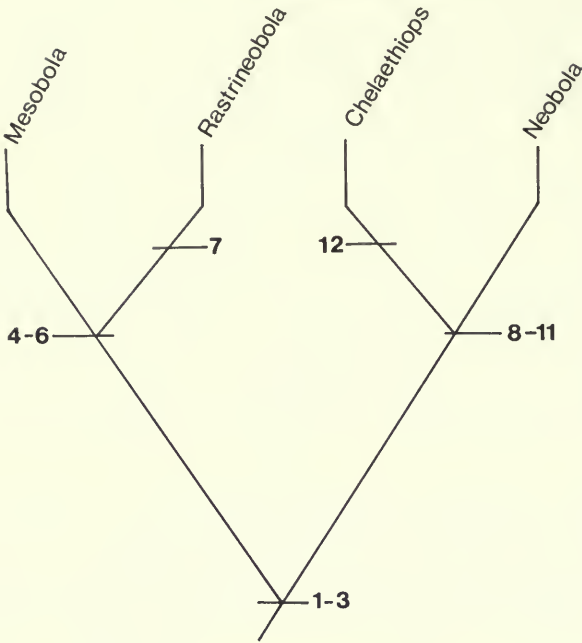


**Fig. 19** Characteristics of *Chelaethiops* species: A, *C. bibie*; B, *C. elongatus*; C, *C. congicus*; D, *C. rukwaensis*; E, *C. minutus*. The arrows indicate specific features; length and shape of snout, inclination of head, prominence of frontal ridge, shape of opercular border.

*Mesobola bredoi* (Poll), 1945, is characterized by a maxilla with a high and narrowly triangular palatine process (Fig. 7E); low number of olfactory lamellae, 8 on each half rosette; 11–13 anal fin rays; lateral line scales 36–39; 12 long gill-rakers; pharyngeal tooth formula: 4.2.1; vertebral number 37–39 (4+12–13+19–21+1). The species is confined to Lake Albert.

*Mesobola moeruensis* (Boulenger), 1915, is characterized by a maxilla with a low, sloped palatine process; 9 long gill-rakers; the lower posterior border of the operculum attenuated; 8 olfactory lamellae on each half rosette; 15 branched anal fin rays; lateral line scales 41; pharyngeal tooth formula, unknown; vertebral number 38 (4+12+21+1). All characters taken from a syntype.

A sample of 10 specimens from Katanga (MRAC 85812–847) named as this species, have gill-rakers less spinose than those of the type specimen and more closely resembles *M. spinifer*. *Mesobola moeruensis* is most probably confined to Lake Mweru, and those samples from elsewhere named as this species belong to some other taxon.



**Fig. 20** Above, synapomorphy scheme of the neoboline group. Synapomorphies are, 1, channelled supraethmoid; 2, frontal canals at edge of the bones with extensive, laterally opening pores; 3, divided  $A_1$  muscle with complex aponeurotic inclusions; 4, derived ethmovomerine morphology; 5, elongate symplectic; 6, derived jaw morphology; 7, forward shift of jaw articulation; 8, anterior extension of lateral ethmoid; 9, aponeurotic constriction of muscle  $A_{1ant}$ ; 10, enlarged frontal pores; 11, hypertrophied supraneurals; 12, divided  $A_1$  aponeurosis (see text, pp. 179). Below, cladogram showing relationships of the neoboline group. Synapomorphies are, 1, divided  $A_1$  muscle; 2, pectoral axial scales (secondarily lost in some taxa); 3,  $A_1$  *post* muscle insertion divided; 4, derived ethmovomerine morphology (see text, pp. 181).

*Mesobola spinifer* (Bailey & Matthes), 1971, is characterized by a maxilla with a low, sloped palatine process (as in *M. moeruensis*); 7–8 olfactory lamellae on each half rosette; 9–11 gill-rakers on 1st ceratobranchial; 15–16 branched anal fin rays; lateral line scales, 41–45; pharyngeal tooth formula, 4.3.2.; vertebral number 39–41 (4 + 13 + 21 – 23 + 1).

Bailey & Matthes (1971) compare *M. spinifer* with other species here included in *Neobola* and *Mesobola* and conclude that it is most closely related to *M. moeruensis*. They distinguish *spinifer* from *moeruensis* principally on the higher number of gill-rakers. However, in the syntype of *M. moeruensis* I count 9 rakers on the ceratobranchial, not 7–8 as given by Bailey & Matthes. There is no substantial difference in lateral line scales and branched anal fin ray counts. Bailey & Matthes (1971) also distinguish *M. spinifer* from *M. moeruensis* on body depth. The authors give a body depth range of 18.3–21.8% of SL for *M. spinifer* but give no figures for *M. moeruensis*. The body depth for the only examined syntype is 22.8% of the SL and the range for the Katangan specimens of 'moeruensis' (see above) is 21.1–24.7% (mean 23.5%). In numbers of branched fin anal fin rays (16–18) and vertebral count (total 39–40), the Katangan specimens of *M. 'moeruensis'* are closer to *M. spinifer* than to the type specimen of *M. moeruensis*. *Mesobola spinifer* occurs in the Malagarasi and Ruaha drainages (see Bailey & Matthes, 1971).

**SPECIMENS EXAMINED.** *Mesobola brevianalis*: 1907.4.17:90 (holotype), Mkuzi R., Zululand; 1907.5.15:5–7, Devaard R., Transvaal; 1915.6.29:15–17, Aapies R., at Petronella; 1977.6.27:299–300, Namaini Pan, Pongolo R.; 1977.6.27:307–1256, Pongolo R., below Jazini Dam, Mzinyeni Pan, N. Natal; 1982.4.13:4693–97, Sabe R., Chisumbanje, Zim-babwe; 1978.8.3:158–62, L. Chiuta; MRAC 186489–947, Chambesi R., Rhodesia.

*Mesobola bredoi*: 1969.3.18:1–15, Lake Albert.

*Mesobola moeruensis*, 1920.5.26:84 (syntype), Lake Mweru; *Mesobola 'moeruensis'* MRAC 85812–847, Elizabethville, Katanga.

*Mesobola spinifer*: 1970.3.10:1 (holotype), Kazima, Malagarasi watershed; 1970.3.10:2–9; 10–11 (paratypes), same locality as holotype.

### **RASTRINEOBOLA** Fowler, 1936

*Rastrineobola argentea* (Pellegrin), 1904 is the type and only species of the genus. It is characterized by an elongate ethmoid region, short, deep jaws, long gill-rakers, 10 olfactory lamellae on each half rosette, absence of pectoral axial scale and a swimbladder with long anterior and posterior chambers, the posterior curving downward and extending to above the anus.

#### **Cranial anatomy**

**Osteology** (Figs 2, 3 & 5). The ethmoid bloc is long, narrow and deep. The lateral edges of the supraethmoid are raised forming a shallow dorsal channel; posteriorly the bone is overlapped by the frontals. The mesethmoid has an omega-shaped ( $\Omega$ ) indentation, the lateral arms abut on long, anteriorly directed preethmoids. The vomer floors the mesethmoid indentation and its anterior border is also strongly indented. The exposed portion of the vomer, between the mesethmoid arms, is sometimes perforated (Fig. 3E). The lateral ethmoid has a marked lateral protrusion (*cf.* the truncated condition in *Neobola* and *Chelaethiops*) from the frontal margin and is sloped anteroventrally.

The *frontal canal* is common with other neobolines lies on the margin of the bone and has 3 dorsally directed sensory pores; the 4th pore opens laterally. The *nasal* is broad, lacking dorsal pores.

The morphology of the *neurocranium* is essentially like that of *Mesobola* except in having a flatter cranial surface, smaller sphenotic, straighter edged pterotic, longer basioccipital and parietals. The supraoccipital is also shorter than in *Mesobola* and bears a slight crest (Fig. 5). There is a ventral opening between the basioccipital and parasphenoid.

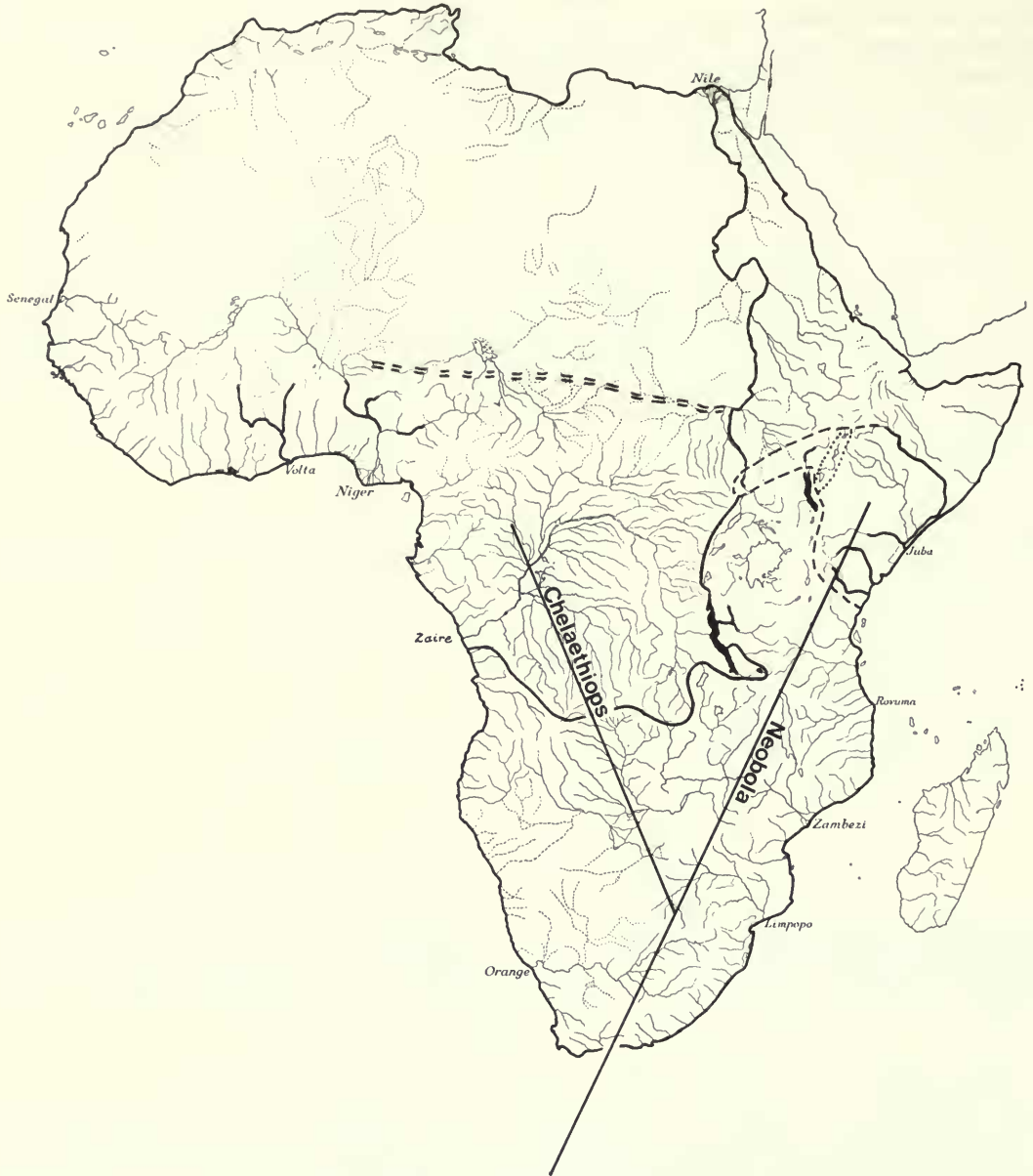
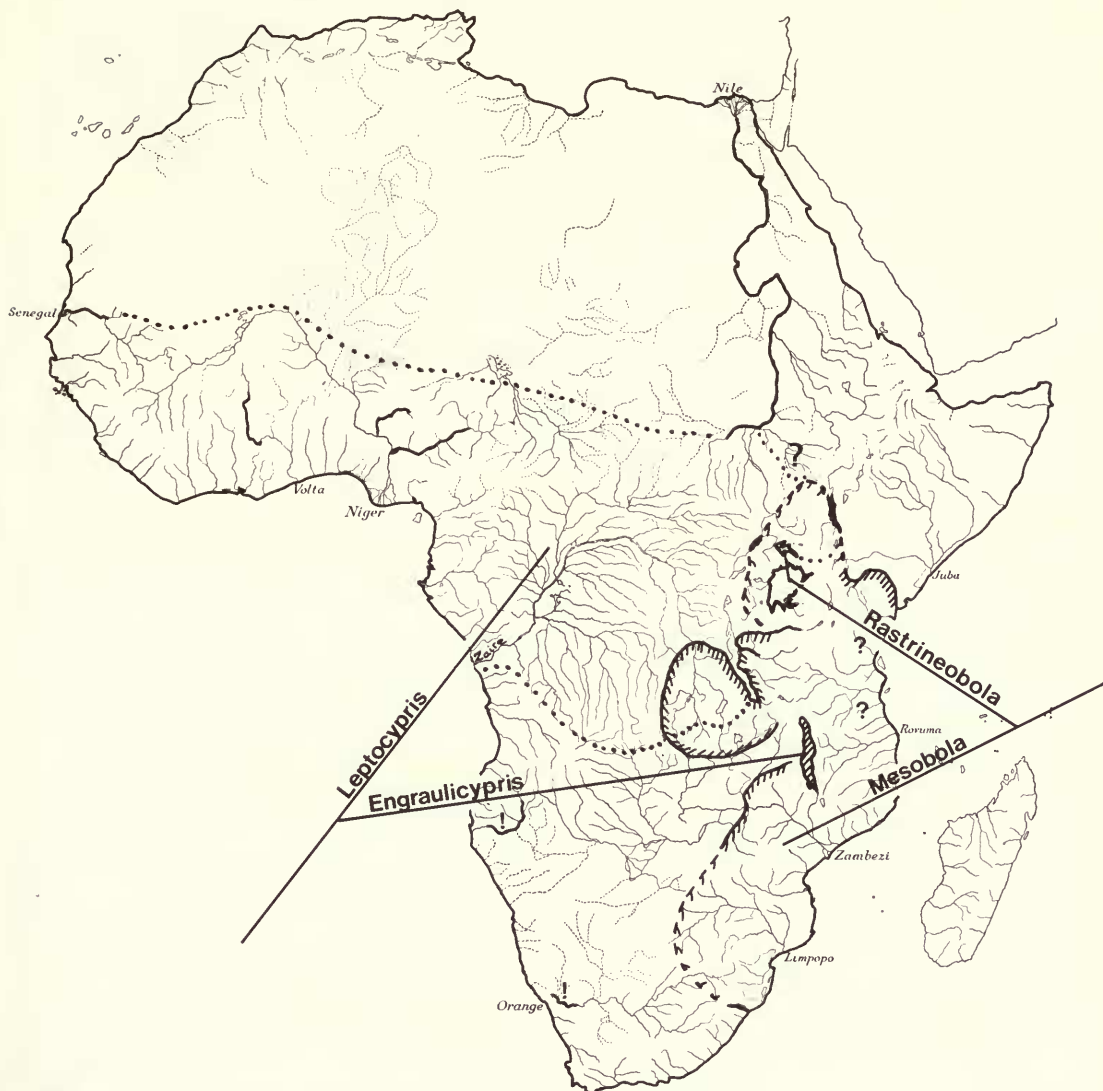


Fig. 21 Distribution of *Neobola* and *Chelaethiops*. The single dashed line indicates the probable limit of *Neobola* distribution; the area enclosed by the dotted line is devoid of any records of *Neobola* species. The Nile marks the eastern boundary of *Chelaethiops*, that in the west is unknown and is indicated as the Volta, the northern extent is marked by a double-dashed line. The lakes where *Chelaethiops* species occur are shown in solid black.

The *infraorbitals* (Fig. 6D) are all of approximately the same depth, the 1st is broadly triangular with the sensory canal passing through its centre, the 2nd bears an antero-dorsal process and the canal, as in the 3rd, 4th and 5th, runs through the centre of the bone. The 5th infraorbital is separated from the wide supraorbital.

The *jaws* (Figs 7 & 8) are shorter than in other neobolines. The maxilla bears a high mid-lateral (palatine) ascending process with a convex (*cf.* concave) posterior border (Fig. 7G).





**Fig. 22** Distribution of *Mesobola*, *Rastrineobola*, *Leptocypris* and *Engraulicypris*. The supposed limits of *Mesobola* species are indicated by hatched lines, the lakes where they occur by solid black. Exclamation signs mark the western records. The Nile is the eastern boundary of *Leptocypris*, while the dotted lines indicate the supposed northern and southern boundaries. *Rastrineobola* occurs only in Lakes Victoria and Kioga, and *Engraulicypris* in Lake Malawi.

Anteriorly the maxilla is not bifurcated as in the other genera where the arms of the bifurcation are of equal length. Instead the medial arm is the longer and is directed ventrally. The ventral border of the maxilla is concave. The premaxilla has a short anterior ascending process. The dentary is deep with a convex dorsal border and a high, rounded coronoid process, halfway along the bone. The anguloarticular is long with a horizontal dorsal surface (Fig. 8D).

*Suspensorium* (Fig. 9D). The hyomandibula is broadly triangular, its anterior edge vertical; the articulatory condyles are widely separated, the intervening border of the bone being gently concave. The metapterygoid bears a well-developed, narrow process which is directed medially and overlies the posterior margin of the entopterygoid. The ectopterygoid

is a short, deep bone (*cf.* long and slender in other neobolines). As in *Mesobola*, the symplectic is elongate with expanded tips and extends the length of the metapterygoid.

*Branchial arches.* The ceratobranchials are short with 12 or 13 long gill-rakers; epi-branchials with 3 or 4; pharyngeal teeth long and recurved, in 3 rows, 4.3.2. Infrapharyngo-branchial 2 is short and almost square, compared with a longer, triangular element in other neobolines.

The *operculum* (Fig. 9D) is long with a sloped and rounded posterior border.

*Myology* (Fig. 14). As in *Mesobola*, the *adductor mandibulae* section  $A_1$  is divided, the anterior part,  $A_{1,ant}$ , originating from the quadrate and inserting musculosly on to the anterior part of the maxilla; the posterior part,  $A_{1,post}$ , originates from the preoperculum to insert in part *via* a long tendon into the medial fascia of  $A_{1,ant}$  and in part on to the dorsal rim of the coronoid process of the dentary.

Muscle  $A_2$  originates from preoperculum and is divided by the *levator arcus palatini*. The muscle inserts *via* a long tendon on to the medial face of the anguloarticular; a small segment of muscle runs from the tendon of  $A_2$  to the medial rim of the coronoid process, this segment is taken to represent  $A_w$  (Fig. 14B).

### Pectoral girdle (Fig. 10D)

The upright part of the cleithrum is short, the tip of the horizontal limb extending to a point below the parasphenoid ascending process. There is a longer upright cleithral lamina than in other neobolines. The coracoid is deeper posteriorly than in any other neoboline and has an irregularly shaped posterior border; there is also a slight fretting of the anteroventral margin in some specimens.

### Vertebral column

The 1st centrum has a flat articular face and long lateral processes; the 2nd and 3rd centra are fused with long, recurved lateral processes. There are 38–40 vertebrae (4 + 16 + 17 + 19 + 1). The caudal skeleton (Fig. 17D) more closely resembles that of *Chelaethiops* in having a long 6th hypural; it differs from other neobolines in possessing a bifurcate or trifurcate spine on the fused ural centrum, a bowed epural and anteriorly expanded neural spine on the 1st preural centrum. There is a long hypurapophysis.

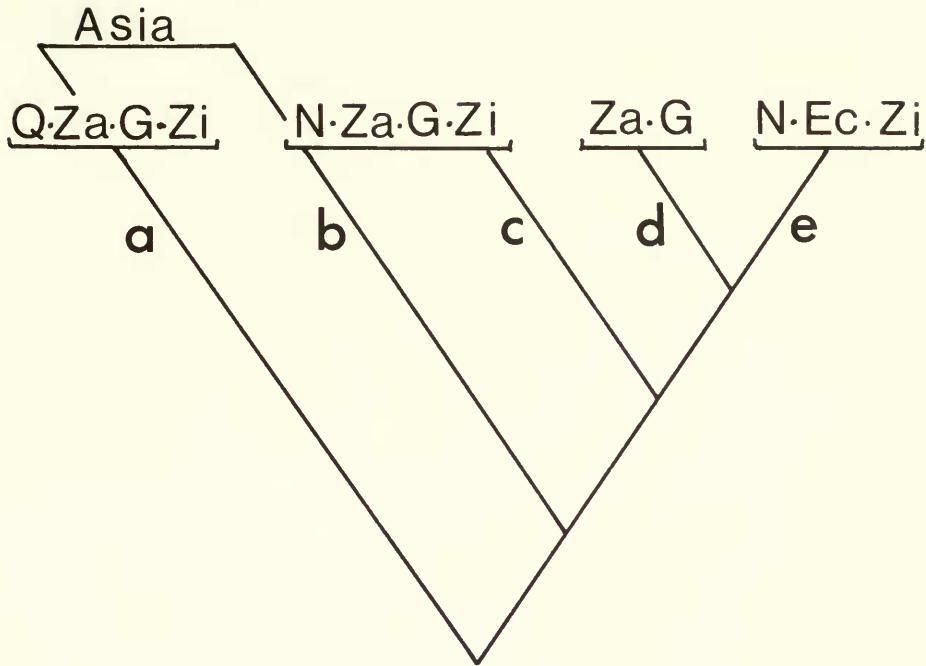
### Taxonomy

There is a considerable variation in lateral line scale counts in the several samples examined. Also, there is a higher range of branched anal fin rays in a sample from Lake Kioga than in those from Lake Victoria. The compared samples are, however, small and it is possible that there may be a greater overlap of minimum values than those indicated:

LOCALITY	N	SL RANGE (MM)	SCALES IN LL.	MEAN	ANAL RAYS
Mwanza	51	49.0–70.0	42–56	50	12–14
Entebbe	20	38.5–78.7	44–56	49	12–14
Lake Kioga	13	38.0–52.6	40–54	49	14–16

In the sample from Entebbe the largest specimen examined, 78.7 mm SL, has 51 scales compared with 56 in a specimen 52.5 mm SL.

**SPECIMENS EXAMINED.** *L. Victoria*: 1905.2.28:2–8 (syntypes), Kavirondo Bay; 1906.5.30:146–51, Bunjako; 1908.10.19:8, Sesse Island; 1909.7.27:11, Kavirondo Bay; 1909.11.15:20, Kizumu Bay; 1964.2.20:12–18, Entebbe; 1982.9.24:1–10; 41–50, Entebbe; 1982.9.24:31–40, Katebo; 1982.9.24:11–20, Mwanza; 50 specimens measured at Mwanza but not preserved. *Lake Kioga*: 1929.4.16:21–22; 1939.3.8:1–10; 1982.9.24:21–30; 1982.9.24:51–60.



**Fig. 23** Reduced area cladogram of African bariliines and neobolines. a = *Opsaridium* + Asian bariliines; b = *Raiamas*; c = *Leptocypris* + *Engraulicypris*; d = *Chelaethiops*; e = other neoboline genera. EC = East Coast; G = Guinean; N = Nilo-Sudanian; Q = Quanzan; Za = Zairean; Zi = Zambesian.

### Phylogenetic relationships of the neoboline group

#### Monophyly

The assumed monophyly of *Neobola*, *Chelathiops*, *Mesobola* and *Rastrineobola* is based on the following synapomorphies:

1. *Ethmovomerine morphology*. The supraethmoid in all neobolines is narrow and dorsally channelled (see p. 152). The plesiomorphic cyprinid supraethmoid is broad and flat (see Howes, 1981).

Within the neobolines, the most extreme form of supraethmoid channelling occurs in *Mesobola* (Fig. 3D). The width and development of the dorsal channel varies interspecifically in *Chelaethiops* (Figs 3B & C). In *Neobola* the dorsal channel is least developed.

Howes (1979) argues that the overlap of the supraethmoid by the frontals is a synapomorphy for chelines and possibly *Chelaethiops* (*Engraulicypris* of Howes, 1979). However, further study shows a similar condition in several other cyprinid taxa, usually in juveniles, where it is an ontogenetic precursor to the sutured joint of the adult. Where it survives in adults, it must be looked upon as ontogenetic retention and therefore plesiomorphic.

2. *The frontal canals situated at the edge of the bone*. Frontal canals occupy the border of the bone only in neobolines. The sensory canal openings are few (3–5), of large aperture, and in *Neobola* and *Chelaethiops* alone all open laterally (Fig. 2).

The common condition in cyprinids is for the frontal sensory canals to be embedded within the bone, distant from its margin and with small dorsal pores. See Howes, 1981 : 17–18 for an account of the plesiomorphic cyprinid frontal.

3. *A derived jaw muscle morphology*. In all neobolines, the *adductor mandibulae* A<sub>1</sub> section is divided into anterior (A<sub>1ant</sub>) and posterior (A<sub>1post</sub>) segments. A<sub>1ant</sub> originates from the quadrate and inserts on the maxilla; A<sub>1post</sub> originates from the lower part of the preoperculum and inserts variously into the lower jaw bone and rictal tissue (see below).

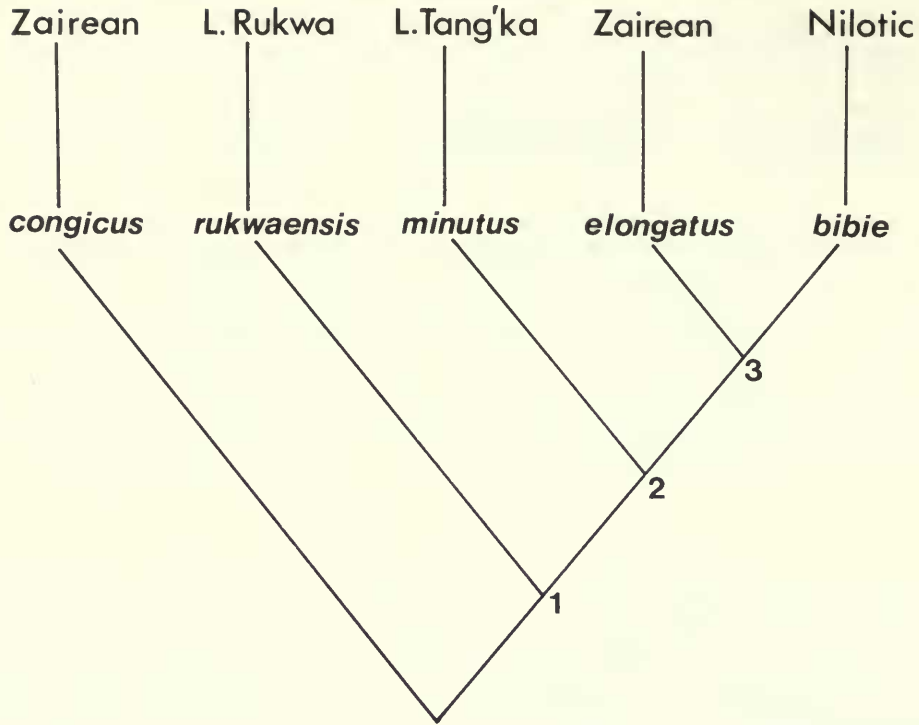


Fig. 24 Cladogram of *Chelaethiops* species. Synapomorphies are 1,  $A_{1post}$  inserts entirely into the dorsal aponeurosis of  $A_{1ant}$ , well-developed frontal canal openings; 2, ethmoid region elongated, dentary with convex margin, articular face of 1st centrum prominently rounded, maxillary valve of increased width; 3, highly developed aponeurotic connection between  $A_{1ant}$  and  $A_{1post}$ , elongate axial scales.

The plesiomorphic cyprinid condition of the *adductor mandibulae*  $A_1$  is an undivided element with a simple insertion on the maxilla (see Takahasi, 1925; Howes, 1982 : 311). The only other cyprinids known to possess a divided  $A_1$  are certain bariliines (see below).

Another, assumed, synapomorphy is the loss of the single pair of uroneurals in the caudal skeleton. All neoboline genera lack these elements that are present in all other cyprinid taxa examined or documented; the only known exception is *Engraulicypris sardella*. It would appear that several sets of uroneurals is a primitive teleost character (see Patterson, 1968). Amongst other otophysans, characoids have up to 3 pairs, and in siluriformes, they are consolidated with other elements of the caudal skeleton (see Fink & Fink, 1981). In those cyprinid genera considered to be plesiomorphic (*Opsariichthys*, *Opsaridium*, *Barilius*), the paired uroneurals are elongate bones extending to the base of the 5th hypural. In the majority of cyprinid taxa the bones are short, triangular or curved elements. On grounds of commonality amongst cyprinids, the loss of paired uroneurals in neobolines should probably be looked upon as a synapomorphy.

### Relationships of neoboline genera

A series of further derived states of those synapomorphies listed above together with other derived features relate the neoboline genera in the following pattern:

*Neobola* and *Chelaethiops* share:

1. *A derived form of the lateral ethmoid.* The dorsal part of the outer wall of the lateral ethmoid is produced anteriorly as a 'shield' covering the posterior portion of the olfactory

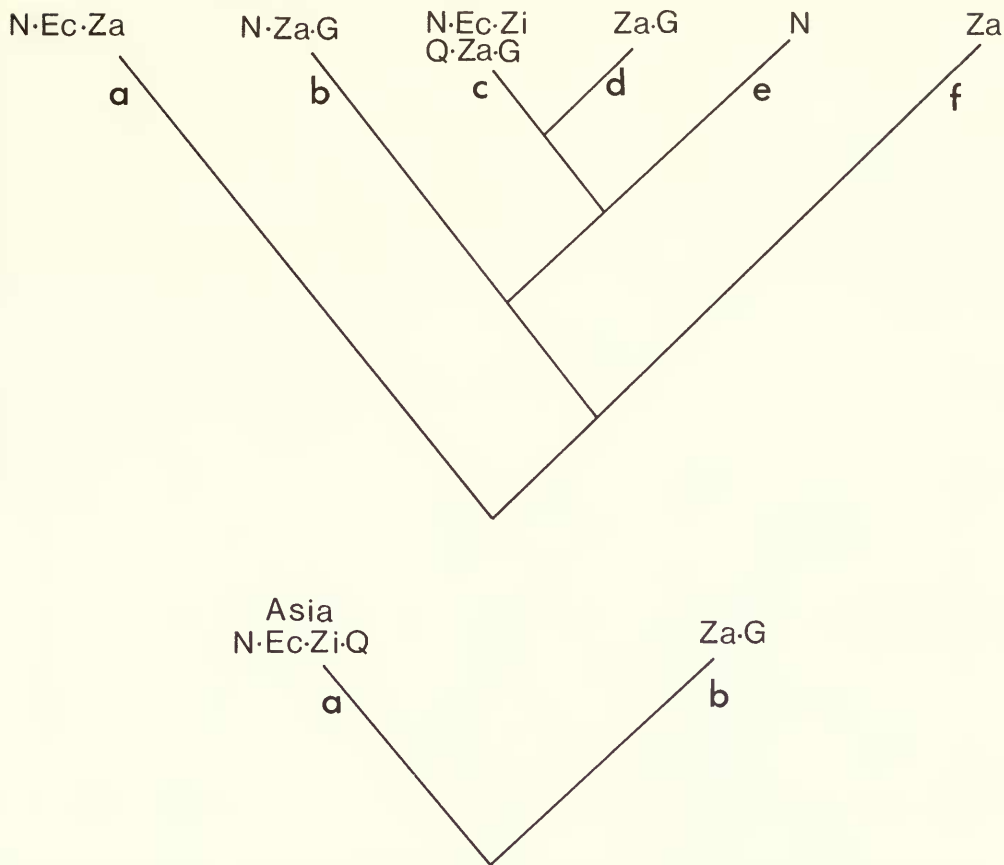


Fig. 25 Reduced area cladograms of (above) Vari's (1979) scheme of distichodontid and citharinid relationships; a-f indicate a = Citharinidae, b = Distichodontidae, Vari's (fig. 47) genera D-E; c = genera G-I; d = genera J-Q; e = *Paradistichodus*; f = *Xenocharax*; (below) Parenti's (1981) scheme for Old-World aplocheiloids, a = other aplocheiloids; b = *Aphyosemion*. Area abbreviations are as in Fig. 23.

organ (see p. 152 & Fig. 4). Elsewhere amongst cyprinids this condition is known only in *Salmostoma*, but here it is the entire lateral ethmoid wall, rather than just the dorsal part, that extends forward. This is probably a parallelism with neobolines in view of the opposing synapomorphy scheme of *Salmostoma* among chelines (see Howes, 1979; 1983).

2. *An aponeurotic constriction of muscle segment A<sub>1</sub> ant.* This configuration of the muscle may be a mechanical device allowing A<sub>1</sub> to circumvent the eye. Otten (1981) presents a diagram hypothesising the functional advantage of A<sub>1</sub> having an aponeurotic sheet in just such a position as occurs in *Neobola* and *Chelaethiops*. In *Chelaethiops* there is a further derived state whereby the aponeurosis is bifurcated.

3. *Enlarged frontal pores opening laterally.* Those in *Chelaethiops* are all laterally directed and the frontal canal is raised above the level of the supraorbital so forming a pronounced ridge in some species (Fig. 19).

4. *Hypertrophied supraneurals.* The supraneurals are plate-like elements. In *Chelaethiops* the bones are larger than in *Neobola*, their most extreme form is encountered in *Chelaethiops minutus* where the anterior 3 or 4 are articulated in a similar fashion to those in some chelines (see Howes, 1979). The presence in *Chelaethiops* of a condylar face on the 1st centrum suggests the facility of cranial elevation, again as in chelines.

*Mesobola* and *Rastrineobola* share:

1. *A derived ethmovomerine morphology.* *Mesobola* and *Rastrineobola* both have a deep mesethmoid indentation which in *Mesobola* is V-shaped and in *Rastrineobola* omega-shaped (see p. 173). In both genera the arms of the mesethmoid abut on long, anteriorly directed preethmoids which, in effect, extend the depth of the indentation. The mesethmoid indentation is floored by the vomer which in both genera is often perforated, the foramen may be small or may coincide with the rim of the overlying mesethmoid. There are also dorsal protruberances of the vomer on either side of the medial notch (Figs 3D & E).

2. *An elongate symplectic.* The cyprinid symplectic is usually a near-triangular bone (the base of the triangle abutting on the lower tip of the hyomandibula). This form of symplectic occurs in *Neobola* and *Chelaethiops* (Figs 9A & B), but in *Mesobola* and *Rastrineobola*, the bone is elongate and horizontal rather than forming the usual steep angle (Figs 9C & D). The tips of the symplectic are spatulate.

3. *A derived jaw morphology.* The maxilla in *Mesobola* and *Rastrineobola* has a tall mid-lateral (palatine) ascending process. In this respect the form of the maxilla is near to that postulated for the presumed plesiomorphic cyprinid type (see Howes, 1981: 28). That this is a secondarily derived form in *Mesobola* and *Rastrineobola* is suggested by the following observations: (i) In *Chelaethiops* and *Neobola*, the sister-taxa to *Mesobola* and *Rastrineobola*, the upper jaw bones are long and slender; the maxilla having a long, low palatine process. This is the characteristic morphology for all bariliines and chelines, considered as the close relatives of the nebolines (see below); (ii) There is a marked concavity of the posterior border of the palatine process, and an acute lateral curvature. These features are absent in plesiomorphic cyprinid maxillae, but present in bariliine and cheline taxa; (iii) The presence of a transitional sequence in *Mesobola* species. In *M. spinifer* the palatine process is long and low, but even so is still higher than that of *Neobola*, *Chelaethiops* and bariliines. In *Mesobola brevianalis* and *M. moeruensis*, the process is taller and more triangular, and in *Rastrineobola*, the palatine process is best developed (Figs 9D–G).

In *Mesobola* and *Rastrineobola* the dentary is deep with a convex dorsal border, a feature particularly marked in *Rastrineobola* (Fig. 8E). In both genera the anguloarticular is long with a horizontal dorsal surface. The usual cyprinid condition, exemplified by *Neobola* and *Chelaethiops* (Figs 8A & C), is for the anguloarticular to be short and deep with a sloped or concave dorsal border. This condition also appears general for teleosts (see Nelson, 1972). In *Rastrineobola* the jaw articulation is situated so far forward that it lies below the anterior half of the orbit (*cf.* below, or posterior to the centre in other nebolines). Only in *Engraulicypris*, amongst bariliines, is the jaw articulation so far forward (see below).

A feature also shared by *Mesobola* and *Rastrineobola* is the elongation and ventral curvature of the posterior chamber of the swimbladder. Comparative out-group data is too sparse to recognize this feature as a synapomorphy, but a brief survey of cyprinids suggest the condition is, at least, unusual.

In summary *Neobola* and *Chelaethiops*, and *Mesobola* and *Rastrineobola* form paired sister groups related on a synapomorphy scheme involving ethmovomerine, frontal, jaw bone, suspensorial and jaw muscle morphology (Fig. 20). The relationships of the nebolines are with certain bariliines.

### Relationships of the neoboline group

The nebolines share with the bariliine genera *Engraulicypris*, *Leptocypris*, *Raiamas* and *Opsaridium* the following synapomorphies:

1. A divided *adductor mandibulae* A<sub>1</sub> muscle. In *Leptocypris* and *Engraulicypris* the fibres of A<sub>1</sub>*post* insert partly into the fascia of A<sub>1</sub>*ant* and partly into the rictal tissue as in the nebolines. In *Raiamas*, *Opsaridium* and South-East Asian *Barilius*, all the fibres of A<sub>1</sub>*post* insert into the fascia of A<sub>1</sub>*ant* (Fig. 15), a condition taken to represent the predecessor of the more complex arrangement in the nebolines, *Leptocypris* and *Engraulicypris*.

2. *Pectoral and pelvic axial scales.* Howes (1983) proposes a fundamental dichotomy of the bariliine group based on axial scale type (*viz.*: elongate 'typical' scales *versus* modified scales in the form of fleshy lobes). Amongst the neobolines, axillary scales are reduced in some species of *Mesobola* and are lacking in *Rastrineobola*. In bariliines, axillary scales are absent in *Engraulicypris*. From the widespread distribution of axial scales amongst neoboline and bariliine genera, it is assumed that their absence in those above cited taxa are independent losses. Where scales are reduced or absent, this condition is confined to lacustrine species.

3. *Derived ethmovomerine morphology.* Amongst the bariliines, only *Leptocypris* and *Engraulicypris* have an ethmovomerine architecture approaching that of the bariliines. In neither genus is there a dorsal channelling of the supraethmoid as in neoboline genera, but in *Leptocypris* there is a slight lateral elevation of the bone (Fig. 3F). In some *Leptocypris* species and in *Engraulicypris* there is an omega-shaped ethmoid indentation, anterior elongation and perforation of the vomer (see Howes, 1980; 1983). These are features shared with the neobolines *Mesobola* and *Rastrineobola*. This pattern of ethmovomerine morphology is disjunct throughout *Leptocypris*, *Engraulicypris* and neoboline species and may, therefore, be a case of homoplasy. Likewise, a somewhat channelled supraethmoid occurs in a group of South-East Asian and Indian *Barilius* species. In these taxa, however, the ethmoid bloc is depressed, rather than laterally compressed as in the neobolines, and other characters such as tubercle pattern and palatine morphology suggest that they form a lineage distinct from that of the neobolines, *Leptocypris* and *Engraulicypris*.

One other feature to be considered is the absence in *Engraulicypris* of paired uroneurals. It was noted above (p. 178) that these elements are lacking in all neoboline genera, and their loss might be construed as a synapomorphy. If this is the case, then *Engraulicypris* would appear to be the sister group to the neobolines, thence to *Leptocypris*. In the synapomorphy scheme presented here (Fig. 20), the caudal fin character has been reserved until such time as more complete comparative data on its distribution are available.

In summary, the neobolines form the sister group to that comprising *Leptocypris* and *Engraulicypris*, which in turn is the sister group to *Raiamas*. This combined assemblage comprises the sister group to the South-East Asian bariliines (possibly including some Indian '*Barilius*' and *Opsaridium*).

### Neoboline distribution and its biogeographic implications

Neoboline taxa have a wide distribution in Africa, embracing the 'ichthyofaunal provinces' Roberts (1975) termed Nilo-Sudanian, East Coast, Guinean, Zambesian and Zairean. *Neobola* species occur in eastern flowing rivers of Ethiopia and Somalia, northern Kenya and in Lake Turkana (Fig. 21). *Chelaethiops*, the derived sister group of *Neobola*, is extensively distributed throughout the Zairean, Guinean and Nilo-Sudanian provinces and also includes Lakes Tanganyika and Rukwa (Fig. 21). *Mesobola* is present in Lake Albert, the Malagarasi, Rufiji and Zambesi systems, and eastern flowing rivers as far south as Natal (Fig. 22). The genus is also known from the Orange River on the western side of Africa, although there is some doubt about the record from the Cunene River; see p. 170. *Rastrineobola* occurs only in the Lake Victoria basin—including Lake Kioga (Fig. 22).

The most notable feature of neoboline distribution is the geographical division of the genera by the eastern Rift system, so that *Chelaethiops* is the only genus with a continuous westward extension. When depicted as an area cladogram, the branching sequence of neoboline taxa shows a sister-group relationship between Nilotic and Zairean areas and East-Coast and Zambesian (Fig. 23). The sister group of the neobolines, *Leptocypris*+*Engraulicypris*, display a congruent area pattern, with Lake Malawi forming the sister-area to the Nilo-Zairean (Fig. 22). Within *Leptocypris*, those species considered as derived, *weynsii*, *lujae* and *modestus*, are Zairean, again a pattern in agreement with that of the derived neoboline, *i.e.* *Chelaethiops*, species; see below.

On the eastern side of the Rift, the area relationship signified by the sister group *Mesobola* + *Rastrineobola*, is between East Coast-Zambesian + Lake Victoria basin.

The distributional pattern of these sister-group pairs is readily explicable on vicariance events involving, in the case of *Neobola* and *Chelaethiops*, the formation of the Rift system, and, in that of *Mesobola* and *Rastrineobola*, the isolation of the latter in the Victoria basin. Roberts (1975) includes Lake Victoria in the East-Coast province, and this geographical relationship is certainly borne out by the neoboline phylogeny.

*Chelaethiops* also occurs in both the Malagarasi and Lake Rukwa. This distribution can either be interpreted as a subsequent dispersal from Lake Tanganyika or, as representing the result of an interrupted (vicariant) distribution due to the topographical evolution of that lake; see Banister & Clarke, 1980. The synapomorphy scheme of *Chelaethiops* species (Fig. 24) makes the latter interpretation more economical. *Chelaethiops congicus* (Zairean) has least derived features and together with *C. rukwaensis* (Lake Rukwa and Malagarasi) and *C. minutus* (Lake Tanganyika) forms the sister group to the derived species *C. bibie* (Nilo-Sudanian) and *C. elongatus* (Zaire-Guinean); see Fig. 24 for character summary.

*Mesobola* occurs sympatrically with *Chelaethiops* in the Malagarasi drainage and the Lualaba, it is also disjunct in distribution, being found in the Orange River below the Aughrabies Falls on the western side of the continent. There is a single, unconfirmed record of its presence in the Cunene (see p. 170). Roberts (1975: 309) supposed this distribution to be the result of dispersal through South-West Africa. It would be more parsimonious to recognise in this pattern the fragmentation of a formerly uninterrupted distribution.

In terms of historical biogeography, the neobolines seem uninformative. This is due partly to the genera resolving only into two-area cladograms, and the mostly unresolved interrelationships of their contained species. Indeed, for *Mesobola*, a species cladogram cannot be constructed as the species are presently recognised only on the basis of mainly, meristic differences. For *Neobola*, of the three species, one, *N. fluviatilis*, is possibly a population variant of another, *N. bottegi*, and the third, *N. stellae* is a lacustrine endemic. The other reason is that there are few cladograms of African freshwater fishes which can be used in broader comparison with neobolines. Only three phylogenies can be considered as a basis for constructing area cladograms; those of Vari (1979), Parenti (1981) and Howes (1983).

Vari (1979) studied the characoid families Citharinidae and Distichodontidae, recognising them as sister groups. Both families are widespread throughout Nilo-Sudanian, Guinean, Zairean, East-Coast and Zambesian provinces. Within the Distichodontidae, most taxa, which according to Vari's scheme of interrelationships are the derived ones, occur in Zairean and lower Guinean regions. As a simplified area cladogram, the distichodontid pattern is one of repeated dichotomy between Nilotic and Zairean-Guinean regions (Fig. 25).

Parenti's (1981) geographical analysis of African aplocheiloid cyprinodonts demonstrates a sister-group relationship between Zairean-Guinean (derived forms) and Nilo-Sudanian, Zambesian-East Coast and Quanzan provinces (Fig. 25).

The bariliine relationships presented by Howes (1980; 1983) show both *Opsaridium* and *Raiamas* with Asiatic relatives and representatives. *Opsaridium* has as its sister group the South-east Asian *Barilius* (and possibly some Indian species, see above, p. 180), and *Raiamas* is represented also in India and Burma. At this high level of universality, the pattern of bariliine distribution is virtually concordant with that presented by Parenti (1981) for Old World aplocheiloids (*cf.* fig. 23 in Parenti with fig. 47 in Howes, 1980). Interestingly, all these patterns – aplocheiloids, characoids, bariliines and neobolines – exclude the Cape Province (see below).

### African ichthyogeography and biotic subdivision

Too few data are available to form any refined picture of African ichthyogeographical history. Those that are available suggest a widespread, plesiomorphic fauna disrupted by



a Zairean-Nilotic break with a subsequent (or even contemporaneous) Zairean-Guinean fragmentation.

To date, studies of African ichthyogeography have been little more than catalogues of endemism and scenarios of dispersals (see Greenwood, 1983 for discussion). The various hypotheses proposed for African freshwater fish distribution are *ad hoc* assumptions based on the supposedly known histories of past drainage patterns. An example of this approach is given by Livingstone *et al* (1982) who account for fish distribution patterns by invoking dispersal from refugia, competition and 'powers of dispersal'. These authors find the '... pattern of faunal similarities surprising...' and rather than accepting that this pattern reflects a previously uniformly distributed fauna (Greenwood, 1983) would prefer to see in it a reflection of '... more recent faunal exchange'.

The same problems have beset discussions of the biogeography of other African faunas and, as for fishes, ecological parameters are seen as the determinate factors in shaping distributional pattern. Two recent examples are works dealing with molluscs (Brown, 1978) and birds (Crowe & Crowe, 1982). According to Brown '... many distributional patterns seem to be dependent mainly on existing ecological conditions'. He does, however, draw attention to the taxonomic relationships between southern east African and Malagasian molluscs. Crowe & Crowe correlate their avian zones with vegetation types, although admitting that the distributional patterns of passerine and non-passerine birds cannot be explained solely on environmental factors; there is no reference to the possible phylogenetic relationships of the respective bird groups.

Similarly, the reasoning behind accounts for mammal distribution has been entirely ecological. Indeed, Rautenbach (1978) emphasises that faunal interrelationships should be interpreted from an ecological point of view. No consideration has been given to a vicariographic approach.

There is a cladistic analysis of African bufonids by Grandison (1981) which shows that the plesiomorphic lineage, represented by *Capensibufo*, is restricted to Cape Province. A reduced area cladogram of the other bufonid taxa also reveals repeated east-west dichotomies. Interestingly, Grandison remarks of *Capensibufo* that it may '... have had an austral origin'.

It was noted above that some groups of cyprinids, characoids and cyprinodonts are congruent in their distribution in being absentees from the Cape Province. The relationships of those freshwater fishes endemic to the Cape are at present largely unknown. According to McDowall (1973) the South African galaxiid, *Galaxias zebratus*, may have a close phylogenetic relationship with *Brachygalaxias bullocki* in Chile, although McDowall would prefer to recognize any affinity between the two as convergence. Reid (pers. comm.) has pointed out that the *Labeo umbratus* group of the Cape may be more closely related to Asian than to other African *Labeo* species.

The ichthyofaunal peculiarities of the Cape are paralleled by its flora. Miller (1982) in reviewing bryophyte distribution concludes that the Cape was '... an island which was left behind and later caught up with the primary continental block...'

It is clear that if the phylogenetic relationships of the endemic Cape fishes were resolved, a general biogeographic pattern for this region would begin to emerge. This example serves to underline Greenwood's (1983) thesis that only by resolving the phylogenetic relationships of African freshwater fishes will any understanding be gained of their present-day distributional patterns.

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